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VOLUME 9 MAY 1940 No. 1

STUDIES ON THE BIOLOGY OF THE EARLY STAGES OF THE SALMON (*SALMO SALAR*)

I. GROWTH IN THE RIVER EDEN

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(*With 5 Figures in the Text*)

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1. INTRODUCTION

SINCE the salmon is a fish of considerable commercial importance it has been the subject of a great many investigations, and its biology has been studied in nearly all the countries in which it occurs. A large proportion of these studies have been based on the examination of the scales either of adult salmon or of migrating smolts; consequently, although a great deal of comparative data exists about such aspects of the subject as can be studied by scale examination, some other aspects of the biology of the salmon have been practically neglected. This applies particularly to the growth, feeding habits, and general biology of the early stages before descent to the sea. For this reason it was decided in 1935 to undertake an investigation of the biology of the salmon during its fresh-water life. After considering various rivers, it was decided to concentrate at first on the salmon of the Eden, since this river could provide a plentiful supply of young fish within convenient reach of the laboratory.

The Eden, which runs through the counties of Cumberland and Westmorland, rises in the northern part of the Pennine range a few miles south of Kirkby Stephen, and flows in a northerly direction to enter the sea at the head of the Solway Firth. Fig. 1 shows the course of the river and the places

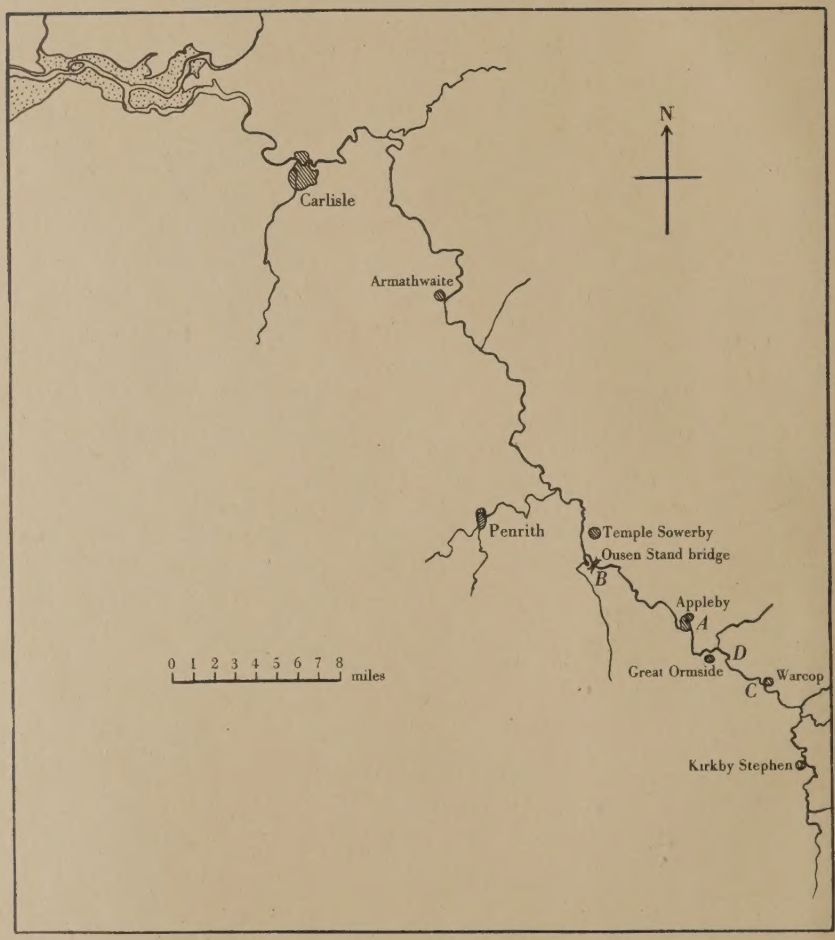

Fig. 1. The course of the river Eden, showing places referred to in the paper.

referred to in this paper. Throughout most of its course the river flows through a wide flat valley floored with alluvium, and the bed of the river consists largely of coarse alluvial gravels. The underlying rock of the drainage area is partly limestone and partly red sandstone. The water of the river is consequently of moderate hardness, and a typical result of analysis is given below:

*p*H	8·2		
Carbonate hardness ...	166	mg./l.	$CaCO_3$
Ammonia	0·05	,,	NH_3
Nitrate	1·7	,,	NO_3
Silicate	3·0	,,	SiO_2
Phosphate	0·007	,,	P_2O_5
Oxygen absorbed ...	2·0	,,	

The greater part of the salmon angling is carried on between Carlisle and Armathwaite. In the autumn, however, the majority of the fish run farther up the river to spawn, and the chief spawning areas on the main river lie between Penrith and Kirkby Stephen; although late-running fish may spawn much farther down river, even as near the sea as Carlisle. It appeared, therefore, that the portion of the river in the neighbourhood of Appleby was the most suitable for the investigation, since it lies in the centre of the chief spawning area and contains a plentiful supply of young fish. It had also the further advantage that in this region the netting operations necessary for the capture of the young fish would not interfere with the salmon angling.

At first, collections were made just above the town of Appleby; but in May 1936 it was decided to make regular collections at two stations some distance apart in order to determine what local variations occurred in different parts of the river. Two stations were therefore selected, one immediately above the Ousen Stand bridge near Temple Sowerby, and the other near the village of Warcop. The station at Ousen Stand was retained until the end of the investigation on the Eden; but at the end of 1936 it became necessary to find another station in place of the one at Warcop, and a stretch of the river near Great Ormside was then chosen. These four netting stations, Appleby, Ousen Stand, Warcop and Great Ormside, are marked *A*, *B*, *C* and *D* respectively in Fig. 1. The distance between Warcop and Ousen Stand by river is 23 km., and between Great Ormside and Ousen Stand 19 km.

2. Methods and apparatus

In any investigation of this type the first problem to be solved is that of the capture of the fish for examination. The principal methods available are: (*a*) by baited hooks, including angling; (*b*) by poisoning or narcotizing; (*c*) by trapping or netting. For any investigation in which the food of fish is to be studied methods including the use of baits are undesirable, since not only is there a risk of the bait appearing among the stomach contents, but also, what

is more important, this method produces a great degree of selection of the fish caught. Poisoning and narcotizing were also inapplicable in the present instance, since not only is the Eden rather large for the use of such methods, but also it was essential that all the trout and the majority of the young salmon caught should be returned unharmed. Some form of netting therefore appeared to be most suitable for the purpose of this investigation.

At first a simple seine was used; but this was found to be unsatisfactory where the current was at all rapid. The apparatus finally used was gradually evolved during the progress of the work and consisted of a modified beam trawl fitted with long wings of netting. In its final form it was efficient in catching fish in a great variety of types of water. The gear and the method of using it are illustrated in Fig. 2. Fig. 2*a* shows the trawl in side view. The runners *ABC* were each made of a single strip of $1\frac{1}{2} \times \frac{3}{16}$ in. (3·8 × 0·5 cm.) spring steel bent to shape and held rigid by a stay *AC* of $\frac{1}{2}$ in. (1·3 cm.) round wrought iron. For convenience of transport the beam was made in two sections, which were bolted together in use. Fig. 2*b* illustrates the trawl from below and shows the shape of the bag. This was constructed of $\frac{1}{4}$ in. (0·6 cm.) knot-to-knot cotton netting and was mounted on 1 in. (2·5 cm.) tanned hemp ropes. The upper and lower surfaces of the trawl carried corks (approx. 5 cm. long × 6 cm. diam.) and leads (approx. 115 g.) respectively, placed as shown.

It was found that the lower surface or floor of the trawl was worn into holes very rapidly by stones caught inside the bag grinding on the gravel of the river bottom. The wear varied in intensity in different parts of the floor, which was therefore divided into three sections, differently constructed according to the intensity of the wear they received. The positions of these sections are indicated in Fig. 2*b*. The first section *ABFG* was floored with an inner layer of the $\frac{1}{4}$ in. netting and an outer layer of $\frac{1}{2}$ in. (1·3 cm.) knot-to-knot netting made of very heavy twine. The centre section *BCEF*, which was found to receive very little wear, was floored with a double layer of the $\frac{1}{4}$ in. netting. Since stones tended to collect at the back of the bag the rear section *CDE* of the floor wore very rapidly, and it was found necessary to construct it of heavy canvas. The inside of the bag was fitted with flaps of netting which formed a funnel to hinder the escape of fish which had entered the bag.

The wings previously referred to were constructed of $\frac{1}{4}$ in. netting, mounted on corked head-ropes and leaded foot-ropes and could be attached to the sides of the trawl, the gap being covered by a flap of netting. They were 4·5 and 18·8 m. long and 1·2 m. deep. A stop-net 37 m. long and 2·1 m. deep, made of the same netting, and heavily corked and leaded, was used in conjunction with the rest of the apparatus.

The method of using this gear is shown in Fig. 2*c*. Owing to the resistance of the fine-meshed netting to the water the nets had always to be moved downstream. The stop-net was placed across the stream at the lower end of

the reach to be netted; it was found best to set the net at a slight angle to the stream as shown in the figure. The trawl and wings were then placed in the stream at the head of the reach with the shorter wing on the side of the stream on which it was intended to beach the trawl at the end of the draw. The gear

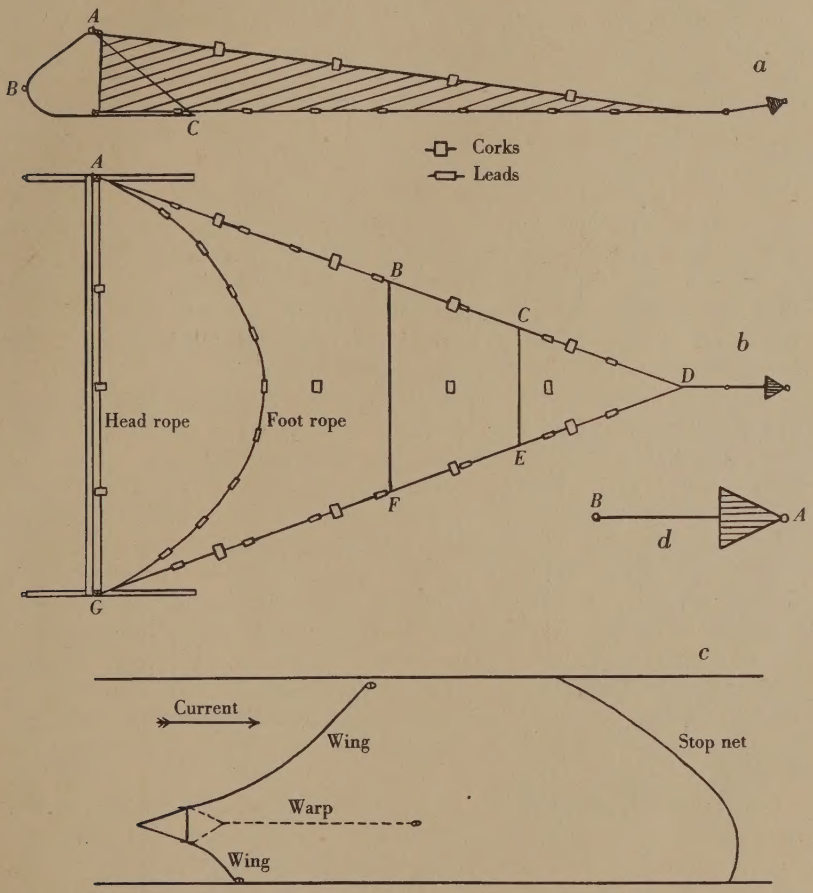

Fig. 2. The apparatus used for catching young salmon in this investigation.

was then pulled steadily downstream by three men, one at the end of each wing and one pulling on warps attached to the runners of the trawl. When the man on the end of the longer wing reached the stop-net, the trawl was kept stationary while the long wing was swept across the stop-net to the other side of the stream. The two wings and the trawl were then hauled ashore.

When the banks were too steep to allow the trawl to be drawn ashore, the wings were gathered in until the trawl was close to the bank, and then the water thus enclosed was violently disturbed to drive all fish present into the bag of the trawl, and the trawl was then lifted out. In order to keep the bag of the trawl extended, and to prevent its being washed down under the beam, a lead weight was attached to the tail. This, which weighed 6·5 kg., was conical in shape, as shown in Fig. 2*d*, and had an iron bar running through the centre. When used in slight currents it was attached by the end marked *A*, but when greater resistance was required it was attached by the end marked *B*. In really rapid currents it was found necessary to dispense with one of the wings, and to have a man holding back the tail with a rope. In water more than about 1 m. deep, a flap of netting 0·6 m. deep, and with corks along the upper edge was attached to the head rope of the trawl. In this case the upper inside corners of the wings were attached to the upper corners of the flap.

This type of gear is quite satisfactory for catching salmon fry after about their second month, but it was found that younger fish hide themselves among the gravel and allow the nets to pass over them. These small fish are best obtained by catching them individually with a small hand-net.

For capturing the very young fry before they have emerged from the gravel of the redds, the method used was to dig up the gravel with a shovel and wash it in a special trough. This trough, which had a wooden bottom and sides, was 90 cm. long by 30 cm. wide by 22 cm. deep. It was divided transversely into two compartments by a partition of $\frac{1}{2}$ in. (1·3 cm.) wire netting 30 cm. from one end. The longer compartment was closed at the outer end with similar netting, the smaller compartment with $\frac{1}{12}$ in. (0·2 cm.) wire gauze. This trough was anchored when required, in a rapid part of the stream, in water about 10–15 cm. deep, with the larger compartment upstream. The gravel believed to contain young fish was then poured gradually into the larger compartment, and as it sank, the lighter material, including the fry, was washed through into the lower section, while the stones were retained in the upper section. In this way the fry could be removed quickly and effectively from a large quantity of gravel.

In the growth studies the fish caught were measured in the field by means of a measuring board of the usual pattern, lengths being read to 0·1 cm. Length was measured from the nose of the fish to the end of the shortest caudal fin ray. Before 1937 only those fish which were brought back to the laboratory for examination of their stomach contents were weighed. During 1937 all fish caught were weighed as well as measured in the field, either singly, or, in the case of very small fish, in batches of six or ten. Weights were determined to 0·5 g.

On return to the laboratory the stomach contents of the fish kept were examined. In order to make accurate comparisons between the size of the fish and the quantity and nature of the stomach contents, each fish was again

weighed and measured. Lengths were measured to 0·1 cm., or, for fish less than 5 cm. in length, to 0·05 cm. Weights were determined to 0·1 g. for fish over 5 g. in weight, to 0·05 g. for fish between 2 and 5 g., and to 0·01 g. for fish less than 2 g. Before weighing the fish its surface was dried with filter paper.

After the weighing, the stomach was removed from the fish through an incision in the left side of the body wall. The anterior limb of the stomach was cut off and opened, and the contents removed. These were examined, the components identified and counted, and the range of size of each organism was measured. The stomach contents were next washed on to a filter made of fine bolting silk stretched over cotton-wool, and the water drained off. They were scraped off into a weighed tube, and dried in an oven at about 65° C. for three days and then weighed again. In this way the dry weight of the stomach contents of each fish was determined.

In order to determine whether there was any relation between seasonal fluctuations in the bottom fauna and changes in the nature and quantity of the food eaten by the fish, it was decided to make systematic quantitative collections of the bottom fauna in the river. The collections were made by means of a special scoop constructed for this work. This scoop is illustrated in Fig. 3*a*. It consisted of a strong square frame *ABCD* made of $\frac{1}{2}$ in. (1·3 cm.) square iron. The front *AB* of this frame was formed into a strong cutting edge, and at the back a triangular frame of iron of the same size carried a threaded socket *S* into which could be screwed an ash pole 2 in. (5 cm.) in diameter and 4 ft. (1·2 m.) long. The main frame carried the bags into which the material scooped up was received. As this scoop was used in running water it was essential to prevent the material disturbed being washed away and lost, and a hood was therefore fitted over the main frame. This, which is shown shaded in the figure, was constructed of 20-gauge galvanized iron sheet carried on an iron frame.

In order to ensure that the scoop was worked at the correct angle two runners *AED* and *BFC* of $\frac{1}{4} \times \frac{5}{8}$ in. (0·6 × 1·6 cm.) iron were attached below the main frame. As it was found necessary in heavy gravel for the scoop to be pulled as well as pushed, two strong eyes *G* and *H*, to which a rope could be clipped by means of spring hooks, were attached to the frame of the hood just above the blade. The bag for receiving the catch was made of fine embroidery canvas, but as the weight of stones scooped up at one time was frequently large, an inner bag of strong string netting of 1 in. (2·5 cm.) mesh was fitted. The inside bag took all the weight of the large stones when the scoop was lifted. In order to prevent the outer bag being worn by rubbing on the stones over which it was moved it was surrounded by an open skirt of light canvas. The bags were in the form of open tubes 4 ft. (1·2 m.) long, and were gathered up and tied with cords at the lower ends. The upper ends of the bags were sewn to a frame of $\frac{1}{4}$ in. (0·6 cm.) square iron, which fitted closely inside the main frame of the scoop and was laced to it with wire.

The width of the scoop was 12 in. (30·5 cm.). When a sample was taken the scoop was pushed along the bottom of the river for 2 ft. (61 cm.); thus the standard sample was an area of 2 sq. ft. (0·185 sq. m.). To ensure the scoop being moved the correct distance, a weighted wooden board 2 ft. in length was placed on the bottom of the stream at the side of the area to be sampled,

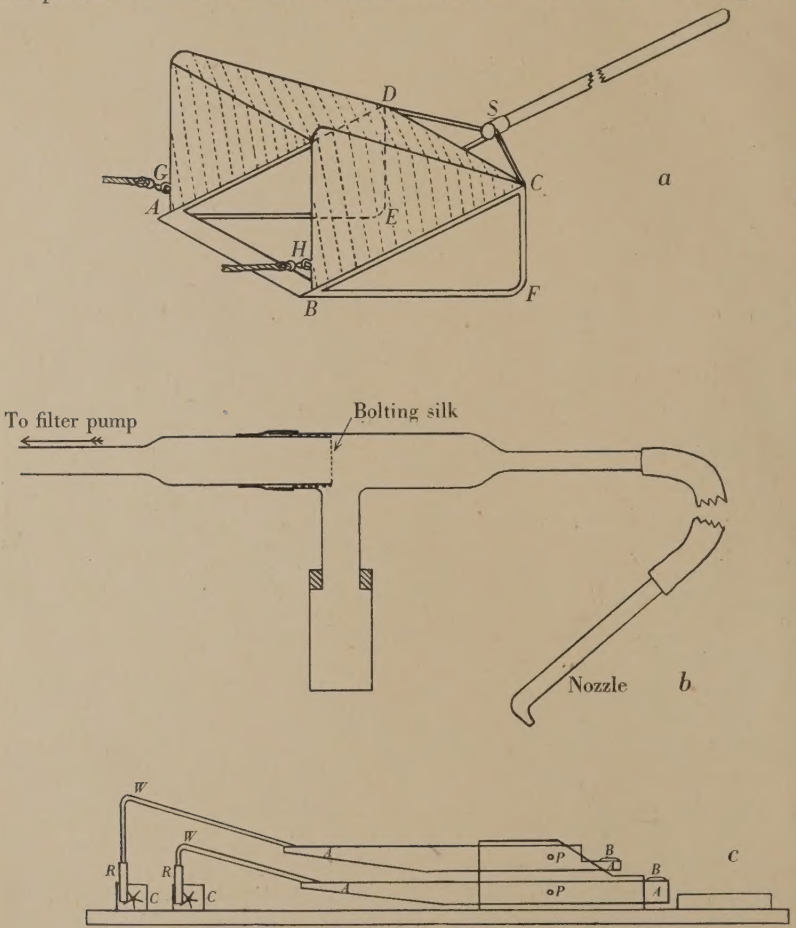

Fig. 3. Some of the apparatus used in the quantitative faunistic work.

with its long axis along the direction of the current. The scoop was then placed facing upstream, with the blade level with the downstream end of the board. After the blade had been pushed into the gravel to a depth of about 7·5 cm., the scoop was forced upstream by two men until the blade reached the opposite end of the board. The scoop was then lifted out.

The material collected was sieved, two sieves being used with meshes of $\frac{1}{2}$ in. (1·3 cm.) and $\frac{1}{30}$ in. (0·08 cm.). The large-mesh sieve fitted inside the smaller mesh one, leaving a space of about 5 cm. between the gauzes. The material from the scoop was emptied into the sieves and well washed. Only material retained between the two sieves was kept; this was placed in canvas bags and taken back to the laboratory, where it was washed in a trough similar to that described by Moon (1935), except that partitions were not used. The washed material was placed a little at a time in a flat white enamel tray, and the animals picked out individually by an automatic pipette which utilized the suction of a filter pump. The pump was connected to a trap, the construction of which is shown in Fig. 3*b*; from the other side of the trap a long rubber tube led to a glass nozzle of the shape shown.

The material in the tray was examined systematically, and whenever an animal was seen it was sucked into the trap. The animals thus isolated were counted in a machine somewhat similar to that described by Ullyott (1937), the trough, however, being moved by a clockwork motor. The number of animals was recorded by means of a counter constructed as shown in Fig. 3*c*. The keys were arranged in two rows of five; each key, which consisted of a wooden arm *AA* working on a pivot *P*, carried at one end a detachable button *B* bearing the name of the animal being recorded by that key, and at the other end a piece of stout wire *W* shaped as shown, and on the end of the wire a piece of rubber pressure tubing *R*. Below each rubber was mounted a cyclometer *C* so placed that the rubber engaged with the starwheel operating it. Pressure on the button raised the rubber clear of the arms of the cyclometer; when the button was released the rubber descended, and engaged and pushed down one of the arms of the starwheel of the cyclometer. Thus each operation of a key increased the reading of the corresponding cyclometer by one.

3. Growth

(*a*) *Length*

The measurements of length are tabulated in Tables 1–3. The mean length and its standard deviation is given for each collection, together with the number of fish measured. Each table shows the results obtained for the fish hatched in one of the three years 1935–7, and is subdivided according to the station from which the fish were obtained. In Fig. 4 the mean length of each collection is plotted against the date.

The results show that growth in length is most rapid in the months June and July, and occurs to a smaller extent in April, May, August and September. In the months October to March practically no growth takes place. There also appear to be distinct differences in the results obtained in different parts of the river. Thus, during June and July 1936, both 1935 and 1936 fish were distinctly larger at Ousen Stand than at Warcop; later in the year this difference disappeared, and finally the Ousen Stand fish were about 0·8 cm.

Table 1. *The mean length, standard deviation and number of fish measured in each collection. Results for fish hatched in* 1935

	Appleby			Warcop			Ousen Stand		
Date	Mean length cm.	S.D. cm.	No. of fish	Mean length cm.	S.D. cm.	No. of fish	Mean length cm.	S.D. cm.	No. of fish
14 June 1935	3·7	0·35	11	—	—	—	4·2	0·23	8
26 June 1935	4·6	0·57	15	—	—	—	—	—	—
26 July 1935	5·6	0·58	11	—	—	—	5·8	0·35	8
16 Aug. 1935	6·7	0·69	22	—	—	—	6·2	0·72	8
11 Sept. 1935	7·4	0·87	27	—	—	—	6·5	0·77	8
4 Oct. 1935	8·6	0·76	4	—	—	—	—	—	—
20–21 Mar. 1936	—	—	—	—	—	—	7·4	0·69	5
8–9 Apr. 1936	8·7	1·02	9	—	—	—	8·3	1·32	10
7 May 1936	—	—	—	—	—	—	8·9	0·87	12
15 May 1936	—	—	—	8·8	0·67	16	—	—	—
27 May 1936	—	—	—	—	—	—	10·1	1·25	17
17 June 1936	—	—	—	10·5	1·16	13	—	—	—
26 June 1936	—	—		—	—	—	11·9	1·11	53
11–12 Aug. 1936	—	—	—	13·6	1·62	17	12·8	1·01	33
1–3 Oct. 1936	—	—	—	14·4	1·14	7	13·1	0·88	26
7–9 Oct. 1936	—		—	14·1	0·93	31	13·5	1·01	40
22–24 Oct. 1936	—			14·2	1·23	35	13·5	1·16	22
5 Nov. 1936	—	—	—	—	—	—	13·6	0·78	10
				Ormside					
14–16 Apr. 1937	—	—	—	13·7	1·63	17	13·6	0·67	9
30 Apr. 1937	—	—	—	13·4	1·66	14	—	—	—
7 May 1937	—	—		—	—	—	15·2	—	2
20 May 1937	—	—	—	14·1	—	4	—	—	—
11–12 June 1937	—	—	—	15·1	—	2	17·1	—	1
23 July 1937	—	—	—	—	—	—	16·0	—	1
23 Sept. 1937	—	—	—	—	—	—	16·8	0·75	6

Table 2. *The mean length, standard deviation and number of fish measured in each collection. Results for fish hatched in* 1936

	Appleby			Warcop			Ousen Stand		
Date	Mean length cm.	S.D. cm.	No. of fish	Mean length cm.	S.D. cm.	No. of fish	Mean length cm.	S.D. cm.	No. of fish
1 May 1936	2·6	0·09	19	—	—	—	—	—	—
6 May 1936	2·6	0·09	20	—	—	—			—
14 May 1936	2·7	0·14	21	—	—	—			
21 May 1936	2·9	0·19	16	—	—	—	—	—	—
28 May 1936	3·0	0·15	12	—	—	—	—	—	—
16 June 1936	3·7	0·38	12	—	—	—	—	—	—
26 June 1936	—	—	—	—	—	—	4·9	0·38	106
3 July 1936	4·7	0·36	40	—	—	—	—	—	—
11–12 Aug. 1936	—	—	—	6·3	0·67	161	6·5	0·67	116
1–3 Oct. 1936	—	—	—	8·2	0·88	30	7·8	0·65	18
7–9 Oct. 1936	—	—	—	8·5	0·77	51	7·4	0·70	34
22–24 Oct. 1936	—		—	8·6	0·84	41	7·8	0·63	17
5 Nov. 1936	—	—	—	—	—	—	7·8	—	1
				Ormside					
14–16 Apr. 1937	—	—	—	8·9	1·25	14	8·5	1·26	10
30 Apr. 1937	—	—	—	8·9	0·80	9	—	—	—
7 May 1937	—	—	—	—	—	—	8·7	0·83	27
20 May 1937	—	—	—	8·8	1·06	51	—	—	—
11–12 June 1937	—	—	—	10·2	1·25	40	11·1	0·89	48
19 June 1937	—	—	—	—	—	—	10·9	0·88	47
23 July 1937	—	—	—	—	—	—	12·6	0·91	41
29 July 1937	—	—	—	12·9	1·34	42	—	—	—
23–24 Sept. 1937	—	—	—	13·5	1·10	27	13·7	0·94	54
18 Oct. 1937	—	—	—	13·4	0·94	24	13·7	1·13	66

Table 3. *The mean length, standard deviation and number of fish measured in each collection. Results for fish hatched in* 1937

	Appleby			Ormside			Ousen Stand		
Date	Mean length cm.	S.D. cm.	No. of fish	Mean length cm.	S.D. cm.	No. of fish	Mean length cm.	S.D. cm.	No. of fish
30 Apr. 1937	—	—	—	2·6	—	2	—		—
8 May 1937	2·6	0·06	12	2·7	0·11	11	—	—	—
13 May 1937	2·8	0·08	10	2·8	0·15	10	—	—	—
19 May 1937	2·8	0·07	10	2·8	0·12	16		—	—
12 June 1937	—	—	—	4·2	0·42	19	—	—	—
19 June 1937	—	—	—	4·2	0·29	44	4·4	0·36	60
23 July 1937	—	—	—	—	—	—	5·7	0·50	33
29 July 1937	—	—	—	6·1	0·66	123	—	—	
23–24 Sept. 1937	—	—	—	7·1	1·04	133	7·9	0·87	58
18 Oct. 1937	—	—	—	6·8	1·24	104	8·0	1·19	86

shorter than those at Warcop. At the end of the growth period in 1937 the Ormside fish were smaller than the Ousen Stand fish, although in this instance the 1937 fish showed a much greater difference than did the 1936 fish. These differences were constant enough to suggest very strongly that there may be real differences in the growth of the fish in different parts of the river.

It has frequently been shown that salmon which migrate to the sea after one year have grown more rapidly during their fresh-water life than those which remain in the river for two or more years; and similarly that two-year migrants have grown more rapidly than those which remain for a third year. As a result of this, length curves such as those in Fig. 4 should show discontinuities at times of migration, that is, in May of each year. The first year of the curve is based on fish which migrate both after one and after more than one year, and these will have a higher average growth rate than the fish whose growth is represented by the second year of the curve, since these are all two- or three-year migrants. Similarly, there should be a discontinuity in May of the third year, since the second year is based on two- and three-year migrants and the third year on three-year migrants only.

In the Eden the great majority of the fish migrate after two years and only small numbers after one or three years. Consequently the discontinuity at the end of the first year should be very slight, since the average growth of all fish during this first year is very close to the average growth of the two-year migrants. On the other hand, the discontinuity at the end of the second year should be pronounced, since the change here is from the average growth of many two-year migrants and a few three-year migrants to the growth of three-year migrants only. Unfortunately, in the present instance insufficient fish in their third year could be collected to show this.

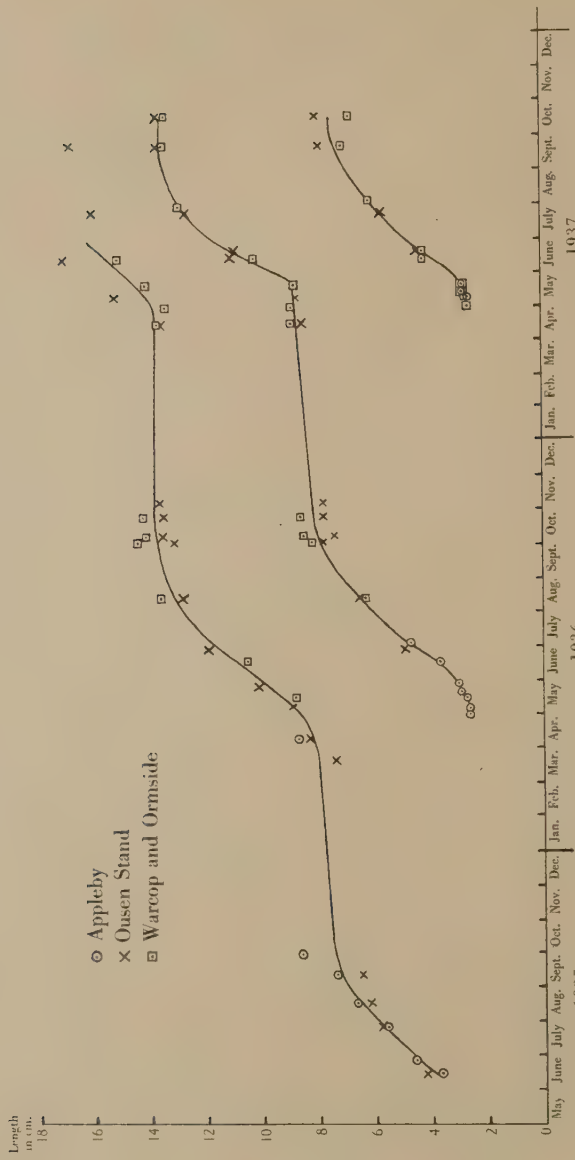

Fig. 4. The mean length of each collection of fish plotted against the date.

(*b*) *Weight*

Tables 4–6 show the mean weight, logarithm (to base 10) of mean weight and mean condition factor (K) of each sample of fish collected during this investigation. The condition factor of a fish is a measure of its weight in relation to its length and is obtained by dividing the weight by the cube of the length. In the present case this figure was multiplied by 10^4 to obtain a number which did not contain a decimal point within the limits of accuracy of its determination.

In the early part of the work only the comparatively few fish brought back to the laboratory were weighed and measured, but from May 1936 onwards all fish caught were measured in the field, although weighing was still done only in the laboratory. Throughout 1937, however, all fish caught were both weighed and measured in the field. The condition factor was calculated for each fish wherever possible, and the mean of the figures thus obtained determined. In some of the 1937 collections when the fish were too small to be weighed individually on the balance used in the field they were weighed in batches, and thus only the mean weight was available. As, however, the lengths of the fish were measured individually the mean cube of the length

Table 4. *The mean condition factor (K), mean weight and log weight of each collection. Results for fish hatched in* 1935

	Appleby			Warcop			Ousen Stand		
Date	K	Mean weight g.	Log weight g.	K	Mean weight g.	Log weight g.	K	Mean weight g.	Log weight g.
14 June 1935	123·5	0·65	1·813	—	—	—	129·0	1·00	0·000
26 June 1935	123·4	1·26	0·100	—	—	—	—	—	—
26 July 1935	135·3	2·46	0·391	—	—	—	134·4	2·61	0·417
16 Aug. 1935	128·0	3·97	0·599	—	—	—	126·9	3·19	0·504
11 Sept. 1935	127·4	5·60	0·748	—	—	—	129·4	3·85	0·586
4 Oct. 1935	125·8	7·30	0·863	—	—	—	—	—	—
20 Mar. 1936	—	—	—	—	—	—	110·4	4·57	0·660
8–9 Apr. 1936	136·6	9·87	0·994	—	—	—	122·6	7·50	0·875
7 May 1936	—	—	—	—	—	—	143·2	10·99	1·041
15 May 1936	—	—	—	139·6	10·14	1·006	—	—	
27 May 1936	—	—	—	—	—	—	149·4	15·55	1·192
17 June 1936	—	—	—	148·3	18·28	1·262	—	—	—
26 June 1936	—	—	—	—	—	—	150·7	25·7	1·410
11–12 Aug. 1936	—	—	—	150·8	39·5	1·597	131·9	27·7	1·443
1–3 Oct. 1936	—	—	—	144·0	41·3	1·616	137·0	29·4	1·468
7–9 Oct. 1936	—	—	—	138·7	39·7	1·599	134·9	32·9	1·517
22–24 Oct. 1936	—	—	—	133·2	38·9	1·590	132·5	32·9	1·517
				Ormside					
14–16 Apr. 1937	—	—	—	113·6	34·8	1·542	115·3	29·4	1·468
30 Apr. 1937	—	—	—	118·3	29·45	1·469	—	—	—
7 May 1937	—	—	—	—	—	—	106·5	37·5	1·574
20 May 1937	—	—	—	114	33·1	1·520	—	—	—
11–12 June 1937	—	—	—	131	45·9	1·662	142	71	1·851
19 June 1937	—	—	—	—	—	—	132	56·25	1·750
23 July 1937	—	—	—	—	—	—	127	52·0	1·716
29 July 1937	—	—	—	126	78·5	1·895	—	—	—
23 Sept. 1937	—	—	—	—	—	—	134	64·0	1·806
19 Oct. 1937	—	—	—	130·3	65·2	1·814	—	—	—

Table 5. *The mean condition factor (K), mean weight and log weight of each collection. Results for fish hatched in* 1936

	Appleby			Warcop			Ousen Stand		
Date	*K*	Mean weight g.	Log weight	*K*	Mean weight g.	Log weight	*K*	Mean weight g.	Log weight
1 May 1936	82·3	0·15	Ī·176	—	—	—	—	—	—
6 May 1936	84·4	0·16	Ī·204		—				
14 May 1936	96·9	0·205	Ī·312	—	—	—			
21 May 1936	105·7	0·26	Ī·415	—	—	—	—	—	—
28 May 1936	112·6	0·32	Ī·505	—	—	—	—	—	—
16 June 1936	120·2	0·66	Ī·820	—	—	—	—	—	—
3 July 1936	122·3	1·22	0·086	—	—	—	—	—	—
11–12 Aug. 1936	—	—	—	125·6	3·35	0·525	122·3	3·45	0·538
1–3 Oct. 1936	—	—	—	126·5	7·04	0·848	131·3	6·41	0·807
7–9 Oct. 1936	—	—	—	125·3	7·90	0·897	128·4	5·39	0·732
23 Oct. 1936	—	—	—	117·7	11·4	1·057	126·5	6·07	0·783
				Ormside					
14–16 Apr. 1937	—	—	—	109·7	9·33	0·970	109·0	7·31	0·863
30 Apr. 1937	—	—	—	114·8	8·53	0·930	—	—	—
7 May 1937	—	—	—	—	—	—	124·1	8·26	0·917
20 May 1937	—	—	—	116·6	8·44	0·926	—	—	—
11–12 June 1937	—	—	—	120·5	13·6	1·135	124·6	17·4	1·241
19 June 1937	—	—	—	—	—	—	127·2	16·6	1·221
23 July 1937	—	—	—	—	—	—	125·7	26·0	1·415
29 July 1937	—	—	—	125·7	27·6	1·440	—	—	—
23–24 Sept. 1937	—	—	—	119·0	30·3	1·482	125·3	32·6	1·514
18–19 Oct. 1937	—	—	—	118·8	28·7	1·458	122·3	32·7	1·514

Table 6. *The mean condition factor (K), mean weight and log weight of each collection. Results for fish hatched in* 1937

	Appleby			Ormside			Ousen Stand		
Date	*K*	Mean weight g.	Log weight	*K*	Mean weight g.	Log weight	*K*	Mean weight g.	Log weight
30 Apr. 1937	—	—	—	96	0·175	Ī·243		—	—
8 May 1937	89·5	0·16	Ī·204	101·5	0·21	Ī·322		—	—
13 May 1937	97·0	0·225	Ī·352	87·5	0·19	Ī·279	—	—	—
19 May 1937	107·8	0·242	Ī·384	101·4	0·225	Ī·352		—	
12 June 1937	—	—	—	101·0	0·77	Ī·881	—	—	—
19 June 1937	—	—	—	111·0	0·82	Ī·914	113·0	0·95	Ī·978
23 July 1937	—	—	—	—	—	—	123	2·39	0·378
29 July 1937	—	—	—	116	2·67	0·427	—	—	—
23–24 Sept. 1937	—	—	—	141	4·13	0·616	114	5·77	0·761
18–19 Oct. 1937	—	—	—	107	3·67	0·565	109	5·85	0·767

was calculated and thus the mean condition factor obtained. The weights of individual fish in a sample of the same age vary so much more than do the condition factors that a far more reliable mean can be obtained for the latter than the former. Consequently the mean weights for the collections made between June and December 1936 were calculated by determining the mean value of *K* for the fish weighed and measured in the laboratory, and multiplying this by the mean cube of the lengths of the larger number of fish measured in the field. The mean weight obtained in this way is probably considerably more reliable than the mean of the small number of fish actually weighed.

In Fig. 5*a* the log weights for the Ousen Stand and Appleby collections are plotted. The results from Ormside and Warcop are not included, since as

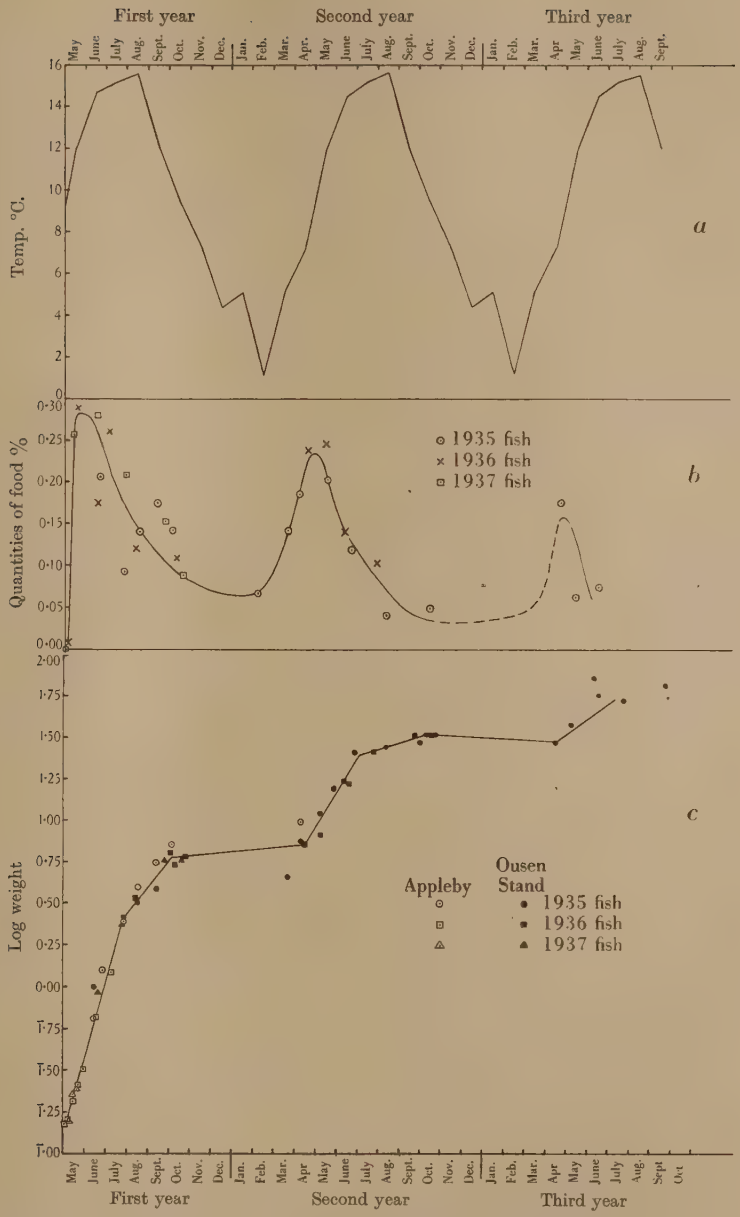

Fig. 5. The monthly mean temperature, the quantity of food and the logarithm of the weights plotted for the two years of fresh-water life.

there are slight differences between the growth at different stations the inclusion of these points tends to mask the shape of the curve. The Appleby and Ousen Stand results however are more or less complementary, since the former principally represent the first two months of the feeding and growing life of the fry, and the latter the remainder of the fresh-water life. The years in the time scale of this figure are years in the life of the fish, so that the position of the points depends entirely on the age of the fish they represent irrespective of the year of hatching or capture. This figure shows that growth in weight follows the same general lines as growth in length. That is, it is rapid in summer, and does not occur in winter. In some cases there appears to be a slight decrease in weight during the winter, corresponding to the decrease in K that takes place at this time. It is noticeable that K tends to be high when growth is rapid and low when growth is slow or non-existent.

The relation between growth in length, growth in weight, and other factors which also show seasonal changes will be considered in a later part of the paper.

4. Quantity of food

In order to make it possible to compare the amount of food in the stomachs of fish of different sizes the dry weight was expressed as a percentage of the weight of the fish. Since the food was dried before it was weighed, and the fish was weighed without drying, this percentage is not the actual percentage which the food in the stomach makes up of the total weight of the fish. It is, however, equally useful as a means of comparison of the amounts of food contained by fish of different sizes. For a number of the more important food animals the proportion of dry weight to live weight was determined, and in the following table the results obtained are expressed as percentages:

Ephemeroptera nymphs (various spp.)	..	19–20%
Plecoptera nymphs	,,	14–15%
Trichoptera larvae	,,	21%
Chironomidae larvae	,,	19–20%

Thus, for a stomach contents which contains a number of different types of food animals the percentage used in this work should be multiplied by 5 or 6 to obtain an approximate value for the true percentage.

In Table 7 the results of the determination of the quantity of food are summarized. For each month during the period of the investigation the mean value of the percentage is given as well as the number of fish examined and the mean date of collection. The results are given separately for fish hatched in the three years 1935, 1936 and 1937. In the case of the 1936 fish two separate results are given for May of that year; the first of these is the mean for two collections made on 1 and 6 May, and the second for three collections made on 14, 21 and 28 May. These results are given separately because on the first two dates only a very small proportion of the fish had begun to feed, while by 14 May feeding had become general.

Table 7. *The mean quantity of food in the stomachs of the fish (Q) expressed as percentage of weight of fish, the mean date and the number of fish examined. The results for fish hatched in different years are given separately*

Year of hatching	1935			1936			1937		
Month	Mean date	No. of fish	Q	Mean date	No. of fish	Q	Mean date	No. of fish	Q
June 1935	20	31	0·221	—	—	—	—	—	—
July 1935	26	19	0·093	—	—	—	—	—	—
Aug. 1935	16	30	0·140	—	—	—	—	—	—
Sept. 1935	11	35	0·175	—	—	—	—	—	—
Oct. 1935	4	5	0·142	—	—	—	—	—	—
Feb. 1936	8	3	0·067	—	—	—	—	—	—
Mar. 1936	20	5	0·142	—	—	—	—	—	—
Apr. 1936	8	19	0·185	—	—	—	—	—	—
May 1936	17	45	0·203	4	39	0·007	—	—	—
,,	—	—	—	20	49	0·289	—	—	—
June 1936	21	25	0·119	16	12	0·174	—	—	—
July 1936	—	—	—	3	11	0·260	—	—	—
Aug. 1936	11	16	0·041	11	21	0·120	—	—	—
Oct. 1936	15	25	0·049	9	59	0·108	—	—	
Apr. 1937	23	13	0·176	20	23	0·238	30	2	0
May 1937	13	4	0·063	14	11	0·246	14	69	0·257
June 1937	17	3	0·075	11	24	0·140	16	22	0·280
July 1937	—	—	—	27	18	0·103	27	18	0·208
Sept. 1937	—	—	—	—	—	—	23	10	0·152
Oct. 1937	—	—	—	—	—	—	19	15	0·088

In Fig. 5*b* the results given in Table 7 are plotted. The years in the time scale are years in the life of the fish as in Fig. 5*c*. It will be seen that the quantity of food rises very rapidly to a very high value as soon as the fish first begin to feed, and then gradually falls during the summer to about one-third of the maximum; it apparently remains at this low value during the winter, and then in April and May there is a rapid rise to a value almost as high as that obtaining in June of the first year. During the late part of the second summer the value again falls off very rapidly to a low winter figure. There appears to be a close correspondence between the amount of food in the stomach and the rate at which the fish is growing.

5. Food supply

Quantitative studies of the fauna of the river were made in order to assist the investigation of the seasonal variations found to occur in the amount of food in the stomachs of the fish. Owing to the difficulty of collecting in the high water which prevailed in the winter months, the most complete series of collections was obtained in the months May to September. As it is in this period that the rapid fall in the amount of food in the stomachs occurs, the results of the collections made in each of these months are summarized in Table 8; the figures represent the average number of animals per square foot of river-bed. It will be seen that there are no significant changes in the quantity of bottom fauna in the river during this period. As will be shown in a subsequent paper, there are great differences in the extent to which different animals in the bottom fauna are used as food by the salmon. By far the

Table 8. *The mean number of animals, of various groups, and of all forms, per square foot for each month from May to September*

Month	May	June	July	Aug.	Sept.
No. of collections	5	2	5	14	4
Ephemeroptera	82	50	168	42	35
Plecoptera	46	136	111	31	12
Trichoptera	34	8	57	70	136
Chironomidae	265	148	256	135	391
Total of above	427	342	592	278	574
Other animals	147	177	144	240	210
Total	574	519	736	518	784

greater part of the animals eaten fall into the four groups Ephemeroptera, Plecoptera, Trichoptera and Chironomidae. For this reason Table 8 contains also the average density of the population of each of these four groups. It can therefore be seen that not only are there no significant changes in the total bottom fauna, but also there are none in that section of the fauna eaten by the fish.

Table 9. *The mean temperature of the water for each month from December* 1935 *to the end of the investigation*

Month	Temp. ° C.	Month	Temp. ° C.	Month	Temp. ° C.
Dec. 1935	2·2	Aug. 1936	15·3	Apr. 1937	7·3
Jan. 1936	2·9	Sept. 1936	12·7	May 1937	10·9
Feb. 1936	1·2	Oct. 1936	9·0	June 1937	14·3
Mar. 1936	6·8	Nov. 1936	7·0	July 1937	15·3
Apr. 1936	7·1	Dec. 1936	6·5	Aug. 1937	16·0
May 1936	13·1	Jan. 1937	7·2	Sept. 1937	11·2
June 1936	15·0	Feb. 1937	—	Oct. 1937	10·0
July 1936	15·0	Mar. 1937	3·6		

6. Temperature changes

From 23 December 1935 until the end of the investigation the temperature of the water of the Eden was read daily, near Appleby, usually between 10.30 and 11.0 a.m. Table 9 records the monthly mean temperatures throughout this period, and in Fig. 5*a* the monthly means are plotted, the results for the different years being taken together.

7. Discussion

It is well known that the rate of growth of most species of fresh-water fish in temperate regions tends to vary to some extent with the season, and the widely used methods of age determination by the study of scales, otoliths, etc., depend on this fact. In the present case, however, the division between the growth and no-growth periods of the year is unusually distinct. The sharpness of the division is clearly shown both in the length curves (Fig. 4) and in the log weight curve (Fig. 5*c*). In the log weight curve the points for both first and second years appear to be grouped about three successive straight lines. Since growth when unaffected by any internal or external change usually follows a logarithmic curve, it appears that the three straight

lines represent three periods during the year in which growth is being controlled by different factors. These periods are:

(*a*) The period of rapid growth; from the beginning of feeding until mid-August in the first year, and from the beginning of April to mid-July in the second year.

(*b*) The period of slow growth; following the rapid growth period, and extending to about the beginning of October in both years.

(*c*) The winter period; with no growth and sometimes a decrease in weight.

Comparison of Figs. 5*b*, *c* shows that there is a clear correspondence between the quantity of food curve and the growth curve. In both years the peak in the quantity of food curve occurs at the beginning of the rapid growth period. This period ends when the quantity of food has dropped to a value about half-way between maximum and minimum, and the succeeding slow growth period ends just before the quantity of food reaches its minimum.

The average amount of food in the stomachs of a number of fish is a good measure of the rate at which they are feeding, although it may be complicated by changes in the rate of digestion. When conditions are such that the rate of digestion is rapid the fish will need to feed more rapidly to maintain the same amount of food in their stomachs than they will when digestion is slow. It is very probable that over the normal range of temperature the rate of digestion in young salmon increases with temperature. When the quantity of food curve is considered in relation to this and to the temperature curve shown immediately above it, it appears likely that the rate of feeding curve would differ from Fig. 5*b* chiefly in that the difference between maximum and minimum would be greater, and that the earlier part of the fall would be less steep and the later part steeper.

Since the correspondence between the rate of growth and the rate of feeding is evidently close, it is very probable that the rate of growth of the fish is directly controlled by the rate of feeding. In this case the factors which control growth are those which control rate of feeding. Such factors could be of three types.

(*a*) External; e.g. changes in the amount of food available.

(*b*) Internal; changes in the feeding behaviour of the fish, due to internal causes.

(*c*) A mixture of external and internal, i.e. changes in the feeding behaviour of the fish in response to changes in the external environment.

Since the fish are inhabiting the same part of the river throughout their fresh-water life, the only purely external factor which could cause the great changes in the rate of feeding would be corresponding changes in the amount of food available, and it has already been shown that these do not occur. Therefore, the changes in the rate of feeding must be attributed to changes in feeding behaviour, due either to internal or to external causes.

In the course of collecting the fish one seasonal change in behaviour was

very clearly observed; this was a change in habitat. During the summer months the young salmon were found scattered throughout the river, although they were most numerous in shallow water between 15 and 75 cm. deep, with a moderate current; but in the winter they could only be caught in the deep still pools. The period which the fish spent in the deep pools was found to be approximately from the end of October to the beginning of April. Table 9 shows that this is the period of the year during which the temperature of the water is below about 7° C. In March 1936 when netting was carried out frequently it was observed that fish could first be caught in shallow water on the very day when the temperature first rose to 7° C. These observations suggest that this may be a critical temperature, above which the salmon lead an active existence and below which they remain quiet. That they are actually quiescent to a great extent during the winter is suggested by the fact that although they can be caught only in the pools at this time, they can be caught during the summer in greater numbers in the same pools. Also the period of pool life corresponds with the period in which feeding is at a minimum and no growth is taking place.

In the spring four events occur practically simultaneously, the rise of temperature to 7° C., the resumption of active life, the rise in the rate of feeding and the commencement of growth. It appears probable that this is a chain of effects each caused by the preceding one, and that thus the commencement of growth in the spring is due eventually to the rise of the temperature above 7° C.

The change from the slow growth period to the period when no growth takes place occurs at the end of October, simultaneously with the return of the fish to the pools and the drop of the temperature to below 7° C. This appears to be a reversal of the spring phenomena, and is further evidence that 7° C. is a critical temperature which marks the change from an inactive, non-growing life to an active, feeding and growing life.

The slowing down of growth in late summer is apparently a separate phenomenon and is clearly linked with the decrease in the rate of feeding which occurs in the latter part of the summer. It has already been shown that the decrease in rate of feeding is not due to any shortage of food. Therefore this change must be due either to some external factor affecting the feeding behaviour of the fish, or to internal changes within the fish itself.

The slowing down in growth takes place after the temperature of the water has been about 15° C. for some weeks. Since the salmon is a fish of temperate regions, it is possible that high temperatures have an adverse effect on the young stages. Donaldson, quoted by Davidson & Hutchinson (1938), has shown that temperatures above 17° C. retard growth and cause excessive mortality in the fresh-water stages of the allied genus *Oncorhynchus*. On the other hand, Alm (1937), working on *Salmo salar*, has shown that in a hatchery there is a direct relation between the mean temperature of the water for the period of

July to September and the size of the salmon fry at the end of their first summer, and he considers 16–18° C. the best temperature for growth. At present there is insufficient evidence to determine whether the slowing down in growth which occurs in the young salmon of the river Eden in late summer is due to the high temperature, or whether some other external factor or an internal factor is the cause.

It has been shown that the weight of the fish follows three successive logarithmic curves in each year. Comparison of growth in weight with the seasonal changes in the condition factor shows that growth in length does not exactly coincide in time with growth in weight. When the young fish first begin to feed there is a rapid increase in the condition factor for the first five or six weeks; during this time the weight is increasing relatively more rapidly than the length. But, gradually, as condition rises, the relative difference in rate of increase disappears, and for a time length and weight increase together and condition remains steady. This effect is well shown in the data for 1936. Condition remains high until the end of the rapid growth period and then decreases slightly during the slow growth period. There is a greater decrease during the winter, and the condition factor is at a minimum just before the recommencement of growth in spring. The recommencement of growth is accompanied by a rapid increase in the condition factor, which reaches its maximum about July and then declines for the rest of the summer. Thus in both years the improvement in condition corresponds with the rapid growth period and the slow decline with the slow growth period. During the second winter period condition again deteriorates until the following spring, when there is a rapid rise at the recommencement of growth.

Thus it appears that at the commencement of a growth period when condition is poor the rate of feeding is rapid, and for a time weight increases rapidly without an equivalent increase in length. Consequently the condition of the fish improves; as the condition factor becomes higher the discrepancy between growth in length and in weight disappears, and finally growth in length becomes equal to growth in weight and condition remains steady. While the fish is growing rapidly the condition remains good, but when at the end of the summer the rate of growth in weight decreases, growth in length tends to continue and consequently condition declines. During the winter when no growth is taking place condition deteriorates greatly.

It appears that there is a close correlation between the condition of a fish and the form that growth takes. When growth is rapid condition is high; if at the beginning of the growth period condition is low growth in weight exceeds growth in length until condition has increased sufficiently. When growth is slow condition is poor, and if originally high is reduced by an excess of growth in length over growth in weight. When no growth is taking place condition declines to an even lower value.

8. Acknowledgements

I must express my gratitude to the Eden Fishery Board for allowing me to net in that river, and to remove young salmon; also to the owners and tenants of numerous fisheries on the Eden for allowing me to work in their waters.

My sincere thanks are also due to Dr E. S. Russell, Director of Fishery Investigations, Ministry of Agriculture and Fisheries; to Prof. W. H. Pearsall, formerly Honorary Laboratories Director of the Freshwater Biological Association; and particularly to Mr W. J. M. Menzies, Inspector of Salmon Fisheries for Scotland; for much help and advice during the progress of this work.

9. Summary

1. This paper deals with some of the results of an investigation made between June 1935 and October 1937 on the biology of the salmon (*Salmo salar*) of the river Eden.

2. The methods used in the investigation are described.

3. It is shown that growth takes place from early April until late October but does not occur during the winter months.

4. When the logarithm of the weight of the fish is plotted it appears that the growth period can be divided into two parts; an early period of rapid growth lasting until mid-August in the first year and mid-July in the second year, and a later period of slow growth.

5. There are great seasonal variations in the quantity of food found in the stomachs of the fish. It rises rapidly to a maximum early in the rapid growth period and then falls steadily during the rest of the summer to a low value at which it remains during the winter.

6. During the summer, when the rate of feeding is decreasing, the amount of food available for the fish remains constant.

7. When the temperature of the water is below 7° C. the young salmon remain quiet in the deep pools; when the temperature is higher they lead an active life in shallower water with a moderate current.

8. It is probable that temperature determines whether growth takes place or not. Below 7° C. the fish are inactive, feed only slowly, and do not grow; above 7° C. the fish are active, feed rapidly, and grow.

9. The change during the summer from rapid to slow growth may be caused either by the high temperature of the water or some other external cause; or else possibly by changes within the fish.

10. There is a close correlation between condition and growth. When growth is rapid condition improves and remains good. When growth is slow condition declines and remains poor. When no growth is taking place condition declines greatly.

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FERTILIZATION IN THE TSETSE FLY, *GLOSSINA PALPALIS*, IN A POPULATION OF LOW DENSITY[1]

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1. Introduction

The tsetse fly, *Glossina palpalis*, was formerly very common in the riverine bush on the Kuja river and its tributaries in the South Kavirondo district of the Nyanza Province, Kenya, but it has been practically eliminated over much of this area. The density of tsetse, as measured by fly rounds,[2] has been reduced from 100 to 200 tsetse per fly-boy-day to about 1 per F.B.D. This measure of control has been obtained using the "Block" method. The riverine bush has been divided into blocks up to several miles long by making clearings of about 1000 yards wide, and in each block the flies have been almost eliminated by "hand-catching"; that is, squads of catchers have patrolled the blocks regularly and caught enormous numbers of tsetse. A full account of the early stages of this work has been published by Symes & Vane (1937), and the present work has been done in the same area described by these workers. The methods of control adopted have two advantages over wholesale clearing, first they preserve much of the bush, and secondly it is much cheaper to catch the flies in a block than to clear the bush. It may be noted that while the "block" method appears successful for controlling *G. palpalis* along rivers and in the bush fringing lake Victoria (Symes & Southby, 1938), it is unlikely to be applicable to other species of tsetse which range widely over the country.

Now, while it has proved practicable to reduce the fly population to very small numbers in these areas, the final eradication of those that remain is very difficult—perhaps impossible—and certainly expensive. We do not know whether the small number left may not increase and re-populate the areas, or whether the fly will die out. It is commonly believed by ecologists that when a population decreases below a certain level it will be unable to maintain itself. There is surprisingly little evidence for this belief, and a study of these greatly reduced tsetse populations should be of some general interest as well as of practical importance.

It has been suggested by K. Mellanby (1937) that some idea as to whether a sparse population of tsetse is likely to maintain itself may be obtained by

[1] Paper published by permission of the Director of Medical Services, Kenya.

[2] The technique of the "fly round" for estimating tsetse density is discussed by Swynnerton (1936). Trained catchers ("fly boys") make a circuit of an area, taking the same time on each occasion, and catch every fly they can. The catch per F.B.D. (fly-boy-day) is approximately proportional to the density of the wild population.

examining the spermathecae of the females captured. It is quite easy to see whether the female has been inseminated (K. Mellanby, 1936), and one fertilization seems to last for life (H. & K. Mellanby, 1937). If practically all the females are being fertilized, then the population may maintain itself or even increase, but if a large number are not being fertilized, then the numbers are presumably so small that the sexes are meeting insufficiently often and it is probable that the population will die out. If after reducing the flies to a certain low level we find that many females are remaining virgin, it may not be necessary to carry out further control measures.

2. Material and methods

Female flies caught in six blocks on the Kuja river or its tributaries were examined. At first all females caught were dissected, but later it was found impossible to do this, and 1737 out of a total of 2956 females were examined. This examination started on 1 July 1938 and continued until the end of December.

The spermathecae were dissected out in the manner suggested by H. Mellanby (1937). They are easily observed and were examined beneath a $\frac{1}{3}$ in. objective. In a fertilized female the spermatozoa are clearly seen by transmitted light as a dark globular mass within the spermathecae (K. Mellanby, 1936). Even if flies have been dead some days there is usually no difficulty in seeing the sperm, though in freshly killed flies they can be more easily seen moving in all directions.

3. Results

Table 1

Area	Total males caught	Total females caught	No. females examined	No. fertile	No. fully pregnant	No. infertile	Percentage infertile	Density per F.B.D. males	Density per F.B.D. females
Block IV	2514	1982	1012	952	122	60	5·92	0·99	0·75
Kibugu	170	126	117	108	18	9	7·70	0·65	0·68
Sare	289	395	369	348	71	21	5·70	0·49	0·61
Block V	610	442	228	213	33	15	6·60	1·43	0·87
Odielo	1	1	1	1	—	—	—	0·05	0·05
Mirogi	9	10	10	8	1	2	20·00	0·04	0·09
Totals	3593	2956	1737	1630	245	107	6·16	Av. 0·61	Av. 0·51

The results of the dissections are summarized in Table 1. It will be seen that in the first four blocks, from which numerous females were obtained, the percentage of infertile females is approximately the same in each case. There is no evidence that a higher percentage of infertile females was to be found in the more sparsely populated areas. The results from the "Mirogi" block are interesting. Here the density was exceedingly low, and it will be noticed that 20% of the females were infertile. However, as this 20% only

refers to two individuals no conclusions can be drawn, and the fact that 80 % of the females were fertile indicates that comparatively satisfactory meeting between the sexes occurs.

It is quite easy, by their general appearance and "feel", to distinguish recently emerged tsetse flies (usually spoken of as "young" flies) from those which have taken at least one meal of blood ("old" flies). Unfortunately full records of the percentages of young and old flies which had not been fertilized were not kept. Most of the infertile females were young, but some were old, the figures available showing that between 15 and 20 % of the virgin females were old flies. As the vast majority of the flies captured were old, and as only about 6 % of the total were not fertilized, the number of old ones which falls into this category is a very small one.

On two occasions the spermathecae appeared to be empty in the case of flies which had larvae *in utero*. Some females were seen to have one spermatheca empty and the other full. I have discussed these points with Dr K. Mellanby, who thinks the spermathecae may have been pressed in such a way that the sperm was forced into the duct where it would be invisible.

Generally the spermathecae contained a large mass of sperm, but in some old flies the spermatozoa appeared to be rather scanty.

4. Summary

Even when a population of the tsetse fly, *Glossina palpalis*, has been reduced to a low level, there is no indication that the males and females are finding difficulty in meeting. There is therefore no evidence that the remaining tsetse population is likely to die out of its own accord.

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THE MORTALITY, FERTILITY AND RATE OF NATURAL INCREASE OF THE VOLE (*MICROTUS AGRESTIS*) AS OBSERVED IN THE LABORATORY

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(*With 2 Figures in the Text*)

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1. Introduction and acknowledgements

This paper forms part of a larger study covering the whole of the work which has been done during the past nine years by the Bureau of Animal Population, on fluctuations in populations of the vole (*Microtus agrestis*). This work was initiated and has been directed throughout by Mr Charles Elton, and was made possible with the help, at first of a grant from the Darwin Fund of the Royal Society, and later by grants from the Forestry Commission and the Agricultural Research Council. Acknowledgement is made to both these bodies for the financial assistance they have given, and also of the facilities given by Prof. E. S. Goodrich, F.R.S., in the Department of Zoology and Comparative Anatomy, where the Bureau's work has its headquarters. It was designed as a co-operative study in which a group of workers took part. The laboratory and the more theoretical side, of which this forms one section, are complementary to the field investigations, and this combined field and laboratory study was only made possible by the breeding of the vole successfully in captivity by Baker & Ranson (1932). This section is more or less complete in itself, although a number of calculations, in which an attempt was made to link these results of laboratory experience to those observed in the field, have necessarily been reserved until the other sections are published. Moreover, the use of the vole as a laboratory test animal (Ranson, 1934; Wells, 1938) makes it desirable that the normal expectation of life in a healthy stock and the probability of dying at various ages, so far as our present information goes, should be available for other workers.

Throughout we have used the term, "true or stable rate of natural increase", in the same sense it is used in human demography (e.g. Dublin & Lotka, 1925; Kuczynski, 1935). It has been called the Malthusian parameter by Fisher (1930). It is the relative rate at which a population would ultimately increase or decrease, if the observed mortality and fertility were to remain constant in a stable and unlimited environment. In a sense it is an abstract quantity, since both mortality and fertility would be expected to vary in response to changes in the environment and the increasing density of any naturally growing population. But it appears to be by far the most convenient measure to employ and is implicit in any system of rates of death and reproduction which is appropriate, for a given population, to the conditions existing at the time of observation. The "net reproduction rate", or the ratio between the total female births in two successive generations, which has been so extensively used in regard to human populations (see Kuczynski, 1935, for references) is closely related to the true rate of natural increase; but it is a much less satisfactory measure, inasmuch as the unit of time in which it is expressed is that thoroughly unsatisfactory span, the mean length of a generation. With a high relative rate of increase or in any comparative work, the true or stable rate, expressed as so many per head of population per year, week or day, is to be preferred.

As is very usual in work of this kind, a number of additional data had been accumulating during the time these computations were being made. It had been hoped that further experiments might have been arranged in order to clear up several points which were raised as the result of this analysis. Since it appears doubtful whether these can be carried out at present, the remaining data have been given in an addendum at the end of the text, thus completing the information which has been gathered up to the time of publication.

We would like to take this opportunity of thanking all our colleagues in the Bureau, and especially Mr Charles Elton, for their generous assistance at all points where this section of the work overlapped with theirs, and for the many fruitful discussions which resulted. We are also greatly indebted to Prof. M. Greenwood, F.R.S., and Dr J. O. Irwin for their kindness in reading this manuscript and for the valuable help and criticism which we received from them.

2. Sources of the data

The stock of voles, which is bred in this Bureau, was originally started in 1930 with a small number of individuals from Corris, North Wales, mixed with a larger batch from Newcastleton in the Scottish Border country, and since that date no new blood has been introduced. The population appears to be healthy; at no time during this experiment were there any sudden and simultaneous deaths among animals of different ages which would suggest any epidemic infection. During the past two years post-mortem examinations have been made by Dr A. Q. Wells of a large number of the normal stock which

died. The findings were consistently negative; no gross pathological lesions were observed and no pathogenic organisms were isolated. Thus the causes of death are unknown, but the available evidence suggests that this stock can be regarded as a closed community free at any rate from any of the grosser forms of bacterial infection.

The stock was housed in a ventilated cellar with no windows, which was illuminated by artificial light from 100 watt bulbs. No cage was nearer than 4 ft. nor farther than 5 ft. away from the source of light. The light was controlled by a time switch and was on for 15 hr. a day. The mean temperature was 18·7° C.; the maximum being 23·5° C. and the minimum 11° C. The technique of keeping the voles has already been dealt with at length (Ranson, 1934) and need only be described in summary:

(1) The cages used were of wood and measured $12 \times 8 \times 5$ in. deep, had lift-off lids and a zinc tray at the bottom. (2) Granulated peat moss was used as litter. (3) The diet was changed in July 1935 from mangold, mixed corn and hay, to wheat and oats, mixed with vitaminized olive oil with a vitamin efficiency of 600 I.U. of "A" and 85 I.U. of "D" per g.; in addition an excess of hay and water was given. (4) The stock was examined once a week (on Tuesday) when all females were palpated for possible pregnancy.

It has been found impossible, through lack of time and space, to keep records of all the voles born in the laboratory: but from time to time and so far as cage room permitted, certain individuals were selected at random from the existing litters and their life histories recorded. These data, relating to 119 male and female voles, were derived from three main groups of individuals.

(1) 53 male voles which were each placed in separate cages approximately one week after weaning. Unfortunately the exact date of birth was not recorded, but the date they started their separate cage life was known. Since this was around three weeks after birth, and it is certain that the error was in no case greater than ± 2 days, 21 days have been added to the cage-life figures in order to give the total number of days lived since birth.

(2) 32 males used for breeding, each of which was placed in a cage in company with one female. The exact date of birth was known in these cases If the female were to die before the male, it was immediately replaced by another adult of breeding age, between six and twelve weeks, from the existing stock, but the latter is not included in the third group since its exact age might not be known.

(3) 34 females used for breeding in a similar fashion to the males. Thus the 66 members of the last two groups passed the whole of their adult lives paired either to a male or a female of breeding age as the case might be.

These 119 individuals were born at various times during the last five years and, although the conditions under which they were kept were standardized in so far as was possible, some change in longevity might well have occurred. In Table 1 is given the mean length of life, together with its standard error, of each of the three groups, the first and largest being divided into two two-yearly periods.

Table 1

Born during	Group	No. of animals	Mean length of life in days
1933–34	Solitary males	33	215·6 ± 19·27
1935–36	Solitary males	20	245·0 ± 21·34
1936–38	Breeding males	32	243·6 ± 24·06
1936–38	Breeding females	34	248·9 ± 21·14
1933–38		119	237·59 ± 10·884

Testing for homogeneity by the method of the Analysis of Variance (Fisher, 1938), the mean variance between groups with 3 degrees of freedom $=7520{\cdot}2$ and is less than the mean variance within the groups, with 115 degrees of freedom, $=14268{\cdot}9 : z$, which is half the difference between the natural logarithms of the mean variances, $=-0{\cdot}3202$. From Fisher's table of the 5 % points of z, for $n_1=\infty$, $n_2=3$, $z=1{\cdot}0716$; so that the observed value of 0·3202 is quite insignificant.

But although the mean length of life both of solitary and mated males, as well as mated females, appears remarkably consistent when the individuals are thus grouped into fairly lengthy periods of time, it must be mentioned that within these periods certain fluctuations of longevity appear to occur. It has been found impossible to correlate these with any seasonal disturbance, or with any of the alterations of diet which have been introduced from time to time. Likewise the data are not extensive enough to test whether there might have been any differences between the various litters. Although this stock of voles is regarded as homogeneous for the purposes of this analysis, it is realized that these results must remain provisional until further data may accumulate.

3. Life table

The figures for males and females were pooled and the somewhat coarse grouping of an eight weeks interval of age was employed. The results are given in Table 2, where the customary symbols have been used; l_x being the number of individuals who survive to age x and d_x the number dying between the ages x and $x+w$, so that in the present table $d_x=l_x-l_{x+8}$. The d_x distribution is characterized by positive skewness, the mode being less than the mean, and is similar in form to those observed, for example, in the case of vestigial *Drosophila* (Pearl & Parker, 1924) and *Acrobasis* (Pearl & Miner, 1936). These may be contrasted with the more commonly observed, negative-skew distributions represented by such as wild type *Drosophila* (Pearl & Parker, 1924), laboratory mice (Greenwood, 1928) and man; the one type being roughly the mirror image of the other.

The raw data were then smoothed and, although doubtless this could have been done satisfactorily in a number of different ways, the following method was employed. Defining μ_x as the Force of Mortality at age x;

$$-\frac{1}{l}\frac{dl_x}{dx}=\mu_x.$$

If the force of mortality is assumed to be directly proportional to the age and $\mu_x = 2h^2x$, where $2h^2$ is a constant, then by integration

$$l_x = l_0 e^{-h^2 x^2}. \qquad \ldots\ldots(1)$$

Putting $l_x/l_0 = P_x$, and $Q_x = 1 - P_x$,

$$Q_x = 1 - e^{-h^2 x^2},$$

and, by differentiation, $dQ_x = 2h^2 x e^{-h^2 x^2} dx$;

the probability of dying between the ages x and $x+dx$ being given by the right-hand member of the last equation. Then if M be the mean age at death,

$$M = 2h^2 \int_0^\infty x^2 e^{-h^2 x^2} dx,$$

from which, by integration, $M = \frac{\sqrt{\pi}}{2h}$.

Table 2

Age x weeks	Observed d_x	Calculated d_x	Calculated l_x	Observed l_x
3	7	8·74	119·00	119
11	14	16·63	110·26	112
19	27	20·76	93·63	98
27	19	20·89	72·87	71
35	17	18·00	51·98	52
43	18	13·62	33·98	35
51	9	9·18	20·36	17
59	6	5·55	11·18	8
67	—	3·03	5·63	2
75	—	1·50	2·60	2
83	1	0·67	1·10	2
91	—	0·28	0·43	1
99	1	0·15	0·15	1
Total	119	119·00		

$\chi^2 = 5{\cdot}18$; $n = 6$; $P = <0{\cdot}70, >0{\cdot}50$; $l_x = 119{\cdot}73 e^{-0{\cdot}000681126 x^2}$.

In the present case it is assumed for the purposes of calculation that the 119 individuals are the survivors at $x = 3$ of an imaginary batch of animals who are exposed to such a force of mortality from birth, and that those who theoretically would die before $x = 3$ can be neglected. The value of M, estimated from the observed d_x distribution, is 33·957 weeks, whence $h^2 = 0{\cdot}000681126$; and the value of l_0 in equation (1) was adjusted = 119·73 so as to give $l_3 = 119$. The calculated values of l_x are given in Table 2, and in testing the agreement between the expected and observed d_x by means of the χ^2 test, the last six frequencies in each distribution were added together. Since two constants, the total and the mean, have been calculated from the observed data, 2 degrees of freedom are lost; $\chi^2 = 5{\cdot}18$ and for $n = 6$, $P = <0{\cdot}70, >0{\cdot}50$; so that the fit is satisfactory, as judged by this criterion. As a matter of interest, it might be mentioned that the same type of equation has been found to give an excellent fit in the case of 524 female vestigial *Drosophila* (data from Pearl & Parker, 1924).

In order to complete the life table, an estimate was made of the infant mortality from the 490 young who were born alive during the life-time of the 34 mated females. These young were weaned when two weeks old and 424 were still alive, giving the probability of dying within the first two weeks of life, ${}_2q_0 = 0{\cdot}13469$. There remains only the mortality during the third week. Unfortunately, there are no actual data for this period, but the impression left from an extensive breeding experience is that the mortality is very low, and that q_x can be taken as being at a minimum round about the third and fourth weeks of life. Since one week is a short period of time compared with the eight-week unit of grouping which has been employed for the adult life table, it will be sufficiently accurate, instead of adopting some arbitrary figure, to assume that no deaths occurred during the third week and calculate from $x = 3$ onwards;

$$P_x = 0{\cdot}8706295e^{-0{\cdot}000681126\,x^2}. \qquad \ldots\ldots(2)$$

The life table calculated from this equation is given in Table 3, where $q_x = d_x/l_x$ and e_x is the mean expectation of life in weeks of an animal which is alive at age x.

Table 3. *Smoothed life table for male and female voles*

Age x weeks	l_x	d_x	q_x	e_x weeks
0	100,000	13,469	0·13469	29·70
2	86,531	0	0	32·17
3	86,531	6,356	0·07345	31·17
11	80,175	12,091	0·15081	25·33
19	68,084	15,095	0·22171	21·11
27	52,989	15,192	0·28670	17·99
35	37,797	13,087	0·34624	15·61
43	24,710	9,904	0·40081	13·76
51	14,806	6,675	0·45083	12·29
59	8,131	4,039	0·49674	11·10
67	4,092	2,205	0·53885	10·10
75	1,887	1,089	0·57711	9·24
83	798	489	0·61278	8·38
91	309	199	0·64401	7·33
99	110	74	0·67273	5·31

4. Age-schedule of fertility

One of the objects of these experiments was to determine, so far as was possible under laboratory conditions, the fertility of the female vole according to her age, the average size of the litters and the interval between successive pregnancies. To these ends the 34 females who are included in the life table passed the whole of their adult lives paired with a male and thus subject, as we hoped, to the risk of becoming pregnant. Any male dying before the female to which it was mated, was replaced by another of breeding age, between six and twelve weeks, from the existing stock. Of the 34 females, 18 were mated once, 12 twice and 4 three times; a total of 54 "marriages" of which 11 proved to be sterile, a surprisingly high proportion. Ten of these

were first matings; five being presumably due to sterility in the male and five in the female, since in each case the surviving partners afterwards proved to be fertile. The ages at death of these five females were 88, 102, 83, 134 and 267 days; and of the males 99, 82, 149, 47 and 197. Except for the female dying at 267 and possibly the male at 197 days, all these cases of sterility appear to be associated with a life much shorter than the average. The remaining sterile marriage was during the 46th week of life of a female, whose first mating had resulted in six pregnancies.

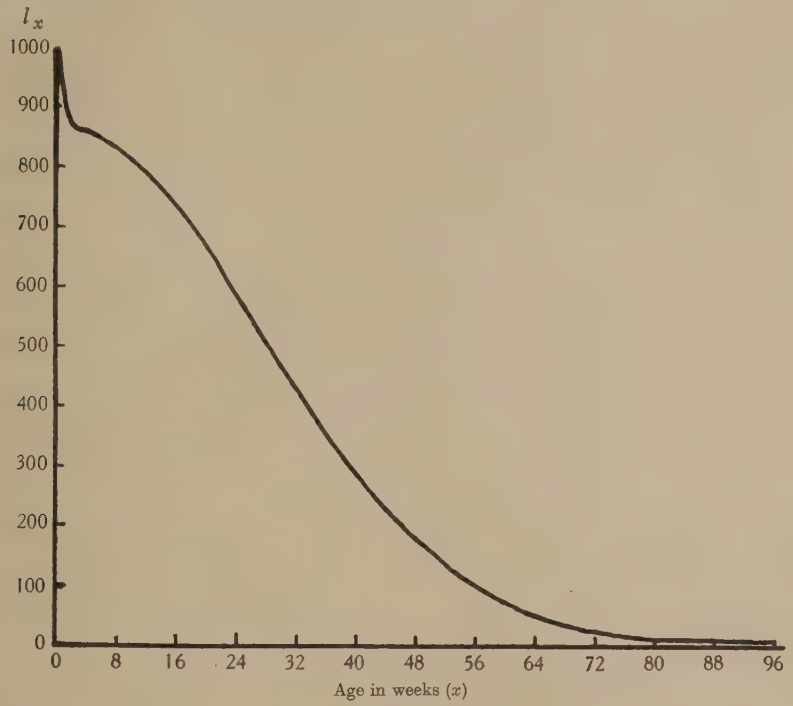

Fig. 1. The smoothed l_x curve, giving the number of survivors out of 1000 individuals born alive, where from the age of three weeks onwards $l_x = 870{\cdot}6295e^{-0{\cdot}000811126x^2}$.

The female vole is known to be fecund at about three weeks old; males, on the other hand, only become potent at about six weeks, as judged by the size of the testes and vesiculae seminales, together with the activity of spermatozoa as seen in microscopic preparations. One of the difficulties in the laboratory has been to obtain a successful mating between a young female aged from three to four weeks and a much older male. In the type of cage used hitherto, such an attempt nearly always resulted in the death of the female; there were, however, exceptions; for instance, at the beginning of

these experiments two females, 33 and 35 days of age, were successfully mated with males aged 111 and 115 days respectively. But such successes were rare, and purely from the point of view of economy it has been the practice to pair a young female with a male of equivalent age and allow them to grow up together. The mean age of the 34 females, when first mated, was $31{\cdot}1 \pm 0{\cdot}8$ days and that of the males, with the exception of the two who have just been mentioned, was $33{\cdot}9 \pm 1{\cdot}4$. On the average these males would have been expected to become potent in about eight days and therefore, since gestation lasts for three weeks, the first litters should have been born round about the 60th day of life of the females. But actually there appears to have been a delay of between three and four weeks in their arrival, the average age of the mothers, in the case of those matings in which both male and female are known to have been fertile, being about 85 days.

It is difficult to give any satisfactory explanation for this quite considerable lag. It may be noted in the case of the two females aged 33 and 35 days who were successfully mated with males aged 111 and 115, that their first litters were born 23 and 20 days respectively after the date on which the individuals were paired. These intervals are entirely compatible with successful copulation occurring between a fertile female and a potent male very shortly after they have been placed in a cage together. But in regard to the 22 males, whose average age when mated was 33·3 days and whose marriage afterwards proved to be fertile, it has been calculated that their average age at the time of conception of their first litters was $68{\cdot}9 \pm 4{\cdot}1$ days, their frequency distribution being:

Age of male at conception of first litter days	Frequency
42–	2
49–	4
56–	3
63–	6
70–	2
77–	1
84–	2
91–98	1
126–133	1
	22

Thus there was a mean difference of about four weeks, with a considerable degree of individual variation, between the age at which on physiological grounds we should have expected these males to have become potent, namely six weeks, and the age at which their first conception occurred. But once breeding had started the litters appeared to follow one after the other at fairly regular intervals. Since gestation lasts for three weeks and it is possible for a female to conceive again the same day on which she gives birth to a litter, it is theoretically possible for a female to have one pregnancy every 21 days of her mated life. In actual practice, however, it is very unlikely that this

figure would ever be realized, since if copulation does not take place on that day or if such a copulation is unsuccessful, there must be an interval, or intervals, during lactation when conception is unlikely to occur. It is suspected that at any rate one and possibly two ovulations may sometimes take place during this period of a fortnight, and of course there may be marked differences between the individual females in the ease with which they conceive during the time they are nursing their young. In order to estimate the average interval between successive pregnancies, the total number of days lived by the females between the dates on which they gave birth to their first and last litters containing live young was divided by the number of litters after the first which were born during that period, including any cases in which the whole litter was born dead. This interval of time between the first and last litters containing live young may be taken as roughly indicating the effective reproductive span in the case of any particular female, and eliminates many of those pregnancies occurring at irregular intervals during the old age of successful breeders in which the embryos are either absorbed or born dead.

Then reverting to the females mated to the 22 males whose ages at the conception of the first litter have already been tabulated, it was found that eleven of them had more than one litter and passed the whole of their lives paired to the same male. They lived a total of 1349 days between their first and last litters of live young, during which time they had 44 pregnancies, an average of 30·66 days per pregnancy. A similar figure of 29·97 days was obtained in the case of the remaining 15 females, mated more than once, and who had a total of 78 pregnancies. Since gestation lasts for three weeks, it follows that on the average these females conceived again about the ninth day after having given birth to a litter. It must be remembered that this figure is averaged over the whole of the reproductive life. Apart from individual differences, we are under the impression that probably the interval is also related to the age of the female.

Throughout the lifetime of the 29 fertile females, 167 pregnancies were diagnosed, an average of 5·75 per female, of which 140 resulted in one or more young being born alive. An analysis of these 27 negative pregnancies, which include those cases in which the whole litter was born dead, showed that three were due to the death of the mother, two were first pregnancies and 15 were associated with the old age of successful breeders. Of the remaining seven, two occurred in females who only lived 174 and 160 days respectively, and no particular qualifications could be attached to the other five.

The 140 litters of one or more live births have been grouped into eight-week periods according to the age of the mother at the time they were born (Table 4). The origin is taken at the age of four weeks, and the mean age of the mothers at parturition estimated from the grouped data is 25·20 weeks (from the individual observations 25·23 weeks). The mean number of live births per litter rises to a maximum and then falls off as the age of the mother increases.

This is comparable to the observations of King (1916) on laboratory-bred rats.

Table 4

Age of mother in weeks	No. of litters	Total no. of live births	Mean no. of live births per litter
4–	12	37	3·08
12–	43	156	3·62
20–	36	133	3·70
28–	25	93	3·72
36–	14	42	3·00
44–	7	22	3·14
52–	2	4	2·00
60–	0	0	—
68–	1	3	—
Total	140	490	3·50

For the purpose of the calculations which are made in the next section, it is necessary to know, not the total number of live young, but the number of daughters who are born. The sex ratio at birth is very difficult to determine with any high degree of accuracy; but the examination of 151 litters at weaning gave 257 males and 248 females ($50{\cdot}89 \pm 2{\cdot}22\,\%$ of males). If it be assumed that the force of infant mortality falls equally on both sexes, the ratio of male to female live births can be taken for all practical purposes as unity.

Table 5

Age group of mother	Observed E_x	Observed no. of daughters	Observed m_x	Smoothed m_x	Expected no. of daughters
4–	33·5	18·5	0·5522	0·6504	21·8
12–	30·5	78·0	2·5574	2·3939	73·0
20–	23·0	66·5	2·8913	2·9727	68·4
28–	17·5	46·5	2·6571	2·4662	43·2
36–	14·5	21·0	1·4483	1·7043	24·7
44–	8·5	11·0	1·2941	1·0815	9·2
52–	4·0	2·0	0·5000	0·6683	2·7
60–	2·0	0	—	0·4286	0·9
68–	1·0	1·5	1·5000	0·3000	0·3
Total		245·0			244·2

$\chi^2 = 1{\cdot}849$, $n = 2$, $P = <0{\cdot}50, >0{\cdot}30$.

E_x = the mean number of females exposed to the risk of having daughters during any particular eight-week age period.

m_x = the mean number of live daughters born per eight weeks per female alive during that age period.

In Table 5 is given the age schedule of fertility derived from the life-histories of the 34 females for whom we have records. This is admittedly a very small sample, but it will be assumed, in default of any other figures, to be representative of the fertility of the female vole under laboratory conditions. Then at the age x, f_x of these females were alive; between the ages of x and $x+8$, d_x died and, as an approximation, the average number of females who were alive during the eight weeks can be taken as $f_x - \frac{1}{2}d_x = E_x$, or the average

number exposed to the risk of having daughters during any particular eight-week age period. The total number of daughters who were born is taken from Table 4 and, when divided by E_x, gives m_x, or the mean number of live daughters born per eight weeks per female alive during that age period. The observed m_x column was smoothed by a method which is described fully by Elderton (1938, pp. 113 *et seq.*). Essentially this consists in using a series of hypothetical exposed to risk which, when multiplied by the observed m_x, gives a new distribution of daughters according to the age of the mother. This distribution is then graduated by an appropriate member of Pearson's system of frequency curves and the resulting figures are divided by the hypothetical exposed to risk to give the smoothed m_x. In the present instance, the number of survivors out of 34 individuals aged three weeks expected from the smoothed life table at the pivotal ages 8, 16, 24, etc., was used as the hypothetical exposed to risk (E_x').

Age group	E_x'	$E_x'm_x$	Graduated $E_x'm_x$
4–	32·75	18	21·3
12–	28·74	73	68·8
20–	23·11	67	68·7
28–	17·03	45	42·0
36–	11·50	17	19·6
44–	7·12	9	7·7
52–	4·04	2	2·7
60–	2·10	0	0·9
68–	1·00	1	0·3
Total		232	232·0

The $E_x'm_x$ distribution was graduated by a type III Pearson curve, the equation for the ordinates being

$$y = 76{\cdot}95175\left(1+\frac{x}{2{\cdot}281608}\right)^{3{\cdot}761174} e^{-1{\cdot}648474x}.$$

The values of the constants were estimated from the uncorrected moments of the distribution and x is measured in units of eight weeks from the origin at the mode = 19·526336 weeks. The graduated $E_x'm_x$ figures are the corresponding areas calculated in the case of the 4–12 age group by Simpson's rule and the remainder by means of a quadrature formula. Finally these values were divided by E_x' to give the smoothed m_x column of Table 5, and, in order to see whether the method of graduation was satisfactory, they were then multiplied by the observed exposed to risk column to give the expected number of daughters born. In testing their agreement with the observed number of daughters the last four frequencies in each distribution were added together, $\chi^2 = 1{\cdot}849$, which for 2 degrees of freedom—4 degrees of freedom being lost in fitting a type III curve—is a perfectly reasonable value.

How far this table of fertility may be applied to a population of wild voles is a debatable point. The enforced monogamy is obviously artificial. Whereas in the laboratory a female mated with a sterile male must wait until the death

of the latter before being able to become pregnant, in the field she retains the possibility of being fertilized by a potent male. Moreover the postponement of the age at which a female might give birth to her first litter in the laboratory, may have a marked effect upon the rate of increase of a population subject to this particular form of life table. On the other hand, it might be argued that these differences in the marriage customs of laboratory and wild stocks are compensated for by the freedom of the former from predators, and the more harmful features of the native environment, all of which tend to decrease the expectation of life and therefore the total number of litters born. Moreover, in the laboratory a female can breed continuously throughout her whole life once she is sexually mature: in the field the breeding season is limited roughly to the summer months, and thus a considerable portion of her life may be spent in a state of sexual quiescence. But it will require more data than we have at present to assess the influence of these and other factors. For instance, we know next to nothing about the social habits of the wild vole. Do the individuals pair for the breeding season, or is mating entirely communal? To what extent do different generations interbreed?—a question of obvious importance in the light of the difference between the ages at which males and females become fecund. Until such problems can be answered satisfactorily, it would be rash to draw too close a parallel between the results of laboratory experience and those which might be expected in the field. But, in the meantime, it is possible to study in some detail the structure of a population subject to the marriage laws imposed in the laboratory; to calculate both the rate at which it would increase, and the type of age distribution which would be established, assuming that the observed age schedules of mortality and fertility remain constant; and finally the effect upon such a population of an intermittent breeding season. The results may be of some general interest, and we have found them to be of considerable assistance in interpreting the great fluctuations in numbers observed among wild populations.

5. Rate of natural increase

Suppose a population of voles is subject to the observed age schedules of mortality and fertility, both of which are assumed constant and approaching the optimum for the species. Let us imagine that this population is mating all the year round exactly as in the laboratory, is living in a constant environment where no limitations are imposed upon its increase, and is free from any immigration or emigration. Then if N be the number of individuals, $dN/dt = rN$, where r is the coefficient of increase, or Malthusian parameter. This is composed of a positive fraction b, the instantaneous birth-rate per head of population, together with a negative fraction d, the death-rate per head; so that $b - d = r$. It has been shown by Lotka (1925, p. 110, and earlier papers) that such a population will approach a fixed form of age distribution, and that when this

stable or Malthusian age distribution becomes established, the birth-rate and death-rate assume values which are given by the system of equations,

$$1 = \int_0^\infty e^{-rx} P_x m_x dx, \qquad \text{.....(3)}$$

$$1 = b \int_0^\infty e^{-rx} P_x dx, \qquad \text{.....(4)}$$

$$c_x = b e^{-rx} P_x, \qquad \text{.....(5)}$$

where P_x is the probability at birth of being alive at age x; m_x is the maternal frequency defined in the previous section, or the mean number of daughters born per eight weeks per female alive during the corresponding age period; and c_x is the coefficient of age distribution, so that out of a population N, $c_x N dx$ are aged between x and $x + dx$.

Since, in the case considered here, the sex ratio at birth has been taken as unity and both males and females have been included in the same life table, it is clear that the ratio of males to females in the living population will also be unity. In consequence of this equality of the sexes, many of the calculations made both in this section and the next are greatly simplified and can be carried out entirely in terms of the female half of the population. The values of r, b and d thus computed, as well as the resulting age distributions, apply equally well either to the sexes considered separately, or to both sexes combined.

The coefficient of increase

The first of these three equations (3) is used to calculate the value of r and its solution is given in full by Dublin & Lotka (1925). Only the essential steps are given here. Defining the quantity $R_0 = \int_0^\infty P_x m_x dx$, as the ratio between the total female births in two successive generations;

$$R_0 = e^{\int A\, dr}, \qquad \text{.....(6)}$$

where

$$A = \frac{\int_0^\infty x e^{-rx} P_x m_x dx}{\int_0^\infty e^{-rx} P_x m_x dx}.$$

Then expanding e^{-rx} in series and putting

$$R_n = \int_0^\infty x^n P_x m_x dx,$$

$$A = \frac{R_1 - rR_2 + \frac{r^2}{2} R_3 - \frac{r^3}{6} R_4 + \ldots}{R_0 - rR_1 + \frac{r^2}{2} R_2 - \frac{r^3}{6} R_3 + \ldots}$$

$$= \alpha + \beta r + \gamma r^2 + \delta r^3 + \ldots,$$

where, writing for brevity,

$R_n/R_0=\mu_n'$, the nth moment about the origin at zero.

$$\alpha=\mu_1',$$
$$\beta=\mu_1'^2-\mu_2',$$
$$\gamma=\mu_1'^3-\tfrac{3}{2}\mu_1'\mu_2'+\tfrac{1}{2}\mu_3',$$
$$\delta=\mu_1'^4-2\mu_1'^2\mu_2'+\tfrac{2}{3}\mu_1'\mu_3'+\tfrac{1}{2}\mu_2'^2-\tfrac{1}{6}\mu_4',$$

or, by transferring the origin to the mean,

$$\alpha=m,$$
$$\beta=-\mu_2,$$
$$\gamma=\tfrac{1}{2}\mu_3,$$
$$\delta=-\tfrac{1}{6}(\mu_4-3\mu_2^2),$$

where m is the mean of the distribution and μ_n the nth moment about the mean. Then from (6)

$$\log_e R_0=\alpha r+\tfrac{1}{2}\beta r^2+\tfrac{1}{3}\gamma r^3+\tfrac{1}{4}\delta r^4+\ldots.$$

Whereas Dublin & Lotka (1925), working with human populations and with small values of r, found that the terms beyond $\frac{1}{2}\beta r^2$ were negligible, it is necessary in the present case to employ a fourth degree approximation. The smoothed estimates of m_x which were given in the previous section are tabulated against the pivotal ages (x) of the groups 4–12, 12–20, etc., and the values of P_x for these pivotal ages are calculated by means of equation (2). The sum of the product column P_xm_x gives R_0, the ratio between the total female births in two successive generations, and the estimates of α, β, γ and δ calculated from the uncorrected moments of the distribution are given underneath Table 6. The equation for r is

$$492{\cdot}004r^4-170{\cdot}477r^3+57{\cdot}9121r^2-24{\cdot}3461r+1{\cdot}7756707=0. \qquad (7)$$

In finding the value of r, a great deal of tedious arithmetic may be saved by first solving the second degree equation, which may be written as $ar^2-br+c=0$, the required root being

$$r=\frac{b-\sqrt{(b^2-4ac)}}{2a}.$$

Table 6

Pivotal age x	m_x	P_x	P_xm_x
8	0·6504	0·83349	0·54210
16	2·3939	0·73132	1·75071
24	2·9727	0·58809	1·74821
32	2·4662	0·43343	1·06892
40	1·7043	0·29277	0·49897
48	1·0815	0·18126	0·19603
56	0·6683	0·10285	0·06873
64	0·4286	0·05348	0·02292
72	0·3000	0·02549	0·00765
			$R_0=5{\cdot}90424$

$\alpha=24{\cdot}3461$, $\beta=-115{\cdot}8242$, $\gamma=511{\cdot}432$, $\delta=-1968{\cdot}017$.

This result is then taken as a first approximation to the real root of (7) the remaining calculation taking place in successive steps (Whittaker & Robinson, 1932, p. 87).

The required root is 0·087703, which slightly overestimates the value of r, to which the series is approaching. This lies between 0·0861 (the third degree approximation) and 0·0877, but nearer the latter than the former, the error being probably in the last decimal place. In order to be certain that the method of smoothing employed in the previous section had not distorted the facts to any appreciable extent, the whole calculation was carried out again, but this time using the unsmoothed m_x values given in Table 5, with the result that $r=0{\cdot}08769$. It will be sufficiently accurate to take

$$r=0{\cdot}0877,$$

or, in other words, the rate of natural increase is 87·7 per thousand per week.

Mean length of one generation

Since by definition $R_0=e^{rT}$,

where T is the mean length of one generation,

$$T=\frac{\log_e R_0}{r}$$

$$=20{\cdot}25 \text{ weeks.}$$

This figure gives the mean length of a generation between mother and daughter. It does not necessarily follow that it is the same between father and son. But under the system of mating imposed in the laboratory, there would probably be little difference between the two figures, since the average age of the males at the time of the first mating has been shown to be only very slightly older than that of the females.

Birth-rate

Having estimated the value of r, b is most easily calculated by the numerical integration of the right-hand member of

$$\frac{1}{b}=\int_0^\infty e^{-rx}P_x\,dx.$$

Taking intervals of eight weeks with the origin at birth, the values of P_x for the beginning, middle and end of each interval were multiplied by the corresponding values of e^{-rx} and the integral found by Simpson's rule. Since r is relatively large, it was not found necessary to carry the calculation further than the age of 80 weeks:

$$\int_0^{80} e^{-rx}P_x\,dx=8{\cdot}8764,$$

whence $b=0{\cdot}1127,$

and, since $b-d=r$, $d=0{\cdot}0250.$

Age distributions

The stable or Malthusian age distribution immediately follows and advantage may be taken of the integrals which have already been calculated to arrive at a value for b, for by equation (5) the proportion of the population who are aged between x and $x+8$ is

$$c = b\int_{x}^{x+8} e^{-rx} P_x dx.$$

As a contrast to this stable form, the stationary or life table age distribution is given in Table 7. This form would ultimately be established in a population where the birth-rate and death-rate were equal. If the population is imagined to be growing with a fixed life table in a limited environment according to the logistic equation $dN/dt = (r - kN)N$, an upper limit to the numbers (r/k) is gradually approached. The population will, at an infinity of time, become stationary $(r = 0)$, and the birth-rate will be given by the reciprocal of the mean expectation of life at birth, or $1/29{\cdot}70 = 0{\cdot}0337$.

Table 7. *Age distributions*

Age group	Stable or Malthusian	Life table or stationary
0–	577	235
8–	255	212
16–	107	178
24–	41	138
32–	14	97
40–	5	63
48–	1	38
56–	—	21
64–	—	10
72–	—	5
80–	—	2
88–	—	1
Total	1000	1000

Theoretically the Malthusian age distribution is the limit to which the population would tend, if the fixed age schedules of mortality and fertility were to continue indefinitely in an unlimited environment. When this stable form is established, the birth-rate and death-rate should assume the values which have been calculated above, namely 0·1127 and 0·0250 respectively. That is to say, taking one week as a unit of time, and given a population of 1000 females of all ages distributed in the stable form, we should expect 25 of these to die and some 113 daughters to be born. As a matter of interest the distribution was recalculated, using different age-class limits, and, as will be seen below, 65·1 % of the population would be of reproductive age.

The average death-rate per week $(d_x/l_x - \frac{1}{2}d_x)$ for the appropriate age-classes was calculated from the life table and the number of females dying found. The number living follows by subtraction and by applying the smoothed maternal frequencies (m_x) from Table 5 (divided by eight, since these figures

were originally expressed in an eight-week unit of time) the number of daughters born is obtained. The totals of the columns reproduce the expected number of deaths and births very closely, this agreement serving as a check upon the accuracy of the computations made in this section.

	Age group	Stable age distribution (females)	Death-rate per week	No. dying	No. living	$m_x/8$	No. daughters born
	0–	349	0·0373	13·0	—	—	—
Reproductive ages	4–	381	0·0109	4·2	376·8	0·0813	30·6
	12–	167	0·0217	3·6	163·4	0·2992	48·9
	20–	67	0·0325	2·2	64·8	0·3715	24·1
	28–	25	0·0432	1·1	23·9	0·3082	7·4
	36–	8	0·0536	0·4	7·6	0·2130	1·6
	44–	2	0·0639	0·2	1·8	0·1352	0·2
	52–	1	0·0740	0·1	0·9	0·0835	0·1
	Total	1000		24·8			112·9

It will be noticed that the older age groups are not represented in Table 7. This does not mean that there would be no old voles living: but simply that the dilution of the population with young is so great—94 % are under 24 weeks of age—that in a random sample of 1000 individuals the probability of meeting with a vole older than 56 weeks would be very small indeed. It is thus the age distribution of the infinitely large population which is achieved by geometrical increase in an unlimited environment. In this sense it is not realizable, since any possible environment must ultimately be limited. But it may be held to typify the age distribution which is approached by a rapidly growing population, when the density of numbers is relatively low. From this point of view it is of the utmost use in the subsequent calculations.

It will be seen from this section, that the rate of natural increase of the vole under the mortality and fertility existing in the laboratory is relatively very great and corresponds to a power of multiplying about ten times in six months. Although this figure can only be a first approximation considering the small size of the sample from which it has been derived, it is at least hoped that it will prove to be roughly about the right order of magnitude.

6. Influence of an intermittent breeding season

It has already been mentioned that under the conditions of diet, temperature and light which were maintained in the laboratory, the population bred continuously once the individuals were sexually mature. There was no division of the year into a breeding and non-breeding season, such as is found under natural conditions. This study would be incomplete without some allowance being made for the influence of this essential factor upon the rate of increase. An approach to the problem has been made only in the most general terms, taking the laboratory population as a model which is imagined to suffer a series of abrupt changes.

The first and most obvious effect on a population at the onset of the non-breeding season is that the numbers must decline since mortality alone

will now operate; and that the rate of the decline will depend upon the age distribution at the time when breeding ceased. Suppose three populations each of 1000 individuals, the first distributed as to age in the Malthusian, the second in the stationary form, and the third of all 1000 individuals concentrated in the 0–8 weeks of age class. The last may be taken from the point of view of the population as the optimum case. Then take as an example the 577 individuals of the Malthusian age distribution who compose the 0–8 age group, and as an approximation assume that their average age is the pivotal age of the group, namely four weeks. In eight weeks' time the survivors of these 577 individuals will form the 8–16 age group with an average age of 12 weeks. From the life table the probability at the age of four weeks of being alive at the age of twelve ($_8p_4$) is 0·91651 and therefore at the end of the first eight weeks of the non-breeding season these 577 individuals have fallen to 529. By thus operating on the different groups with the appropriate value of $_8p_x$ and totalling the results in eight-week periods of time, it is possible to follow the curve of the survivors out of the original 1000 individuals.

The results are shown in Table 8. If the conventional figure of a 26-week non-breeding season be adopted, it will be noticed that even in the optimum case (curve *A*) approximately 46 % of the population will have died before the beginning of the next breeding season. In the cases of the Malthusian and stationary age distributions, the mortality would be about 53 and 66 % respectively. The steepness of this fall in numbers is, of course, due to the particular type of life table, with the mode of distribution of deaths occurring relatively early in life. It must be remembered also, that in the field with a high density of the population and the influence of predators, the presumption would be of a lowered expectation of life and thus in the case of curve *C* even a steeper fall might be expected. It is hoped that in time enough data will be collected by means of marking experiments to show whether this high mortality during the non-breeding season is realized in the field. For the present it can be stated that on the whole the available evidence confirms the rapidity of this estimated decrease in the winter populations.

Table 8. *Disappearance of a population during the non-breeding season*

A 1000 individuals aged between 0–8 weeks
B Malthusian age distribution
C Stationary age distribution

Time in weeks	Number of survivors		
t	*A*	*B*	*C*
0	1000	1000	1000
8	917	867	766
16	770	693	553
24	593	510	374
32	418	345	236
40	270	215	138
48	160	123	75
56	87	65	38

Although it may be said that the wild vole only breeds for approximately 26 weeks in the year, yet a closer examination of the question suggests that this figure may be extremely variable. On the one hand it is known that from time to time in certain localities some slight degree of breeding occurs during the winter months; and on the other, a few cases have been observed where the winter population, which normally increases in weight and becomes sexually mature sometime in March or April, failed to breed at all during the succeeding summer. The climatic and physiological factors which may cause the onset of sexual maturity in the spring, as well as the related question as to what extent the young born during the early part of the summer manage to grow up and breed in their turn before the end of the season, need not concern us here. For the purpose of constructing, on the basis of the laboratory data, a model subject to approximately the same conditions as in the field, it will be assumed that the conditions, which cause the winter population to become sexually mature, will also affect any young who are weaned during the time these factors continue to operate. Then in the case of a population increasing in a limited environment, the rate of growth in numbers can be taken as approximating to the Malthusian form ($dN/dt = rN$) when the density is relatively low. If, for the sake of simplicity, the beginning of two successive breeding seasons be fixed at two dates exactly one year apart, a population of N_0 individuals can be imagined to increase for t weeks, and the numbers at the end of this time will be

$$N = N_0 e^{rt}.$$

The population will then decrease at a rate dependent on its age distribution. Let P'_{52-t} be the proportion who will be a live after $52-t$ weeks of the non-breeding season. Then the number at the end of one year will be

$$N = N_0 e^{rt} P'_{52-t},$$

and if r_a' be defined as the momentary coefficient of increase per annum,

$$r_a' = \log_e (P'_{52-t} e^{rt}).$$

Table 9

t No. weeks breeding season	Malthusian population				Stationary population	
	$e^{0{\cdot}0877t}$	P'_{53-t}	$P'_{52-t}e^{rt}$	r_a'	P'_{52-t}	r_a'
8	2·0170	0·164	0·3308	−1·1062	0·102	−2·2828
10	2·4037	0·188	0·4519	−0·7943	0·119	−2·1286
12	2·8645	0·215	0·6158	−0·4848	0·138	−1·9805
14	3·4137	0·244	0·8329	−0·1828	0·159	−1·8388
16	4·0682	0·276	1·1228	0·1158	0·182	−1·7037
18	4·8482	0·309	1·4981	0·4042	0·208	−1·5702
20	5·7777	0·345	1·9933	0·6898	0·236	−1·4439
22	6·8854	0·385	2·6509	0·9749	0·267	−1·3205
24	8·2054	0·425	3·4873	1·2491	0·300	−1·2040
26	9·7786	0·467	4·5666	1·5188	0·336	−1·0906
28	11·6534	0·510	5·9432	1·7822	0·374	−0·9835

Two cases have been worked out and the results given in Table 9 and Fig. 2. In the first a population with a Malthusian age distribution and

$r=0{\cdot}0877$, is supposed to breed for varying lengths of time between 8 and 28 weeks. The values of P'_{52-t} were found by interpolation in column B of

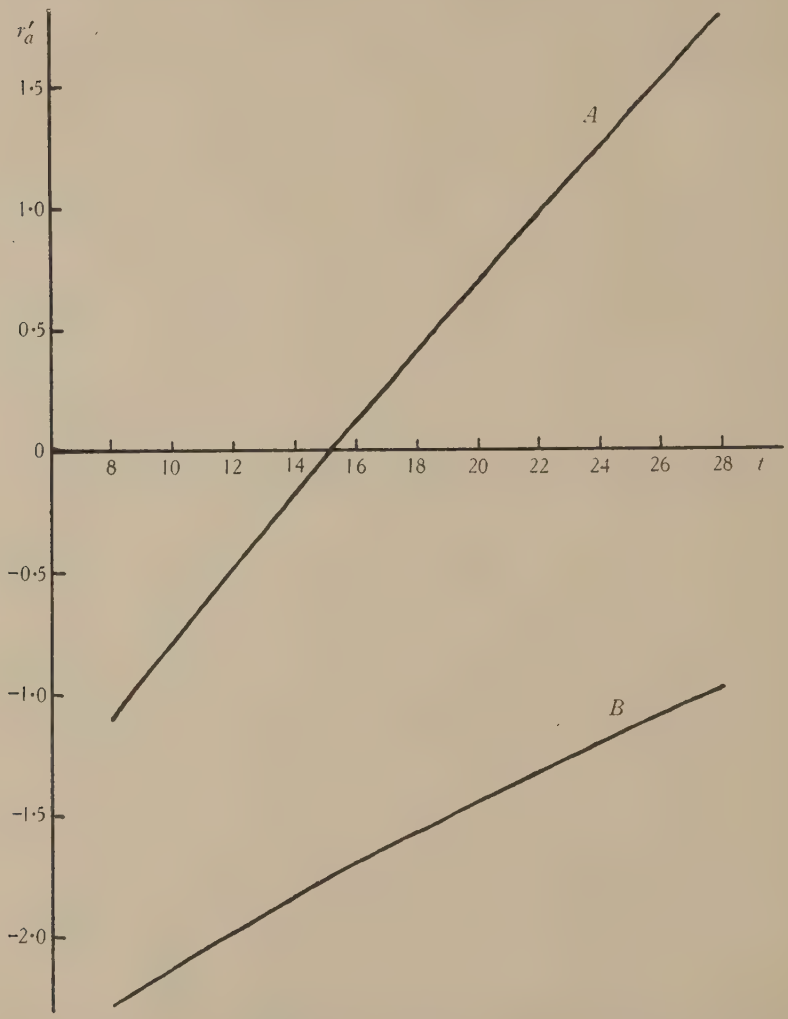

Fig. 2. The relation between the coefficient of increase per annum (r_a') and the length of the breeding season in weeks (t), in the case of a Malthusian population (curve A) and a Stationary population (curve B).

Table 8; and the product column $P'_{52-t}e^{rt}$ gives the number of times the initial population will have multiplied at the end of one year. The comparison

of this column with the second in the table shows how great the summer increase must be in order to obtain even quite a moderate yearly increase. The values of r_a', which start by being negative, rise rapidly as t increases and $r_a' = 0$, in other words the population is the same at the end of one year, when the breeding season lasts for about 15 weeks during which the initial number will have increased between three and four times.

The second case which is considered is that of a stationary population with $r = 0$, in which births are balancing deaths throughout the breeding season. The values of P'_{52-t} are here taken from curve C of Table 8. The estimates of r_a' are naturally always negative, and there is an overlap with the previous curve in the sense that a long breeding season with a stationary population has the same effect upon the yearly rate of increase as a very short season of the Malthusian type. In practice, however, it might be expected that a stationary population would probably breed for a short rather than a long period of time. The curve of r_a' increases relatively slowly as compared with the first case; when $t = 16$, for instance, the population will be reduced to about 18 %, and with $t = 8$ only 10 % will still be alive at the end of the year. In other words, it appears that, if from the beginning of a breeding season the conditions of the environment relative to the density of the population are such as tend to equalize the birth-rate and death-rate, a heavy fall in numbers must be expected.

Strictly speaking, both the Malthusian and the Stationary age distributions are impossible at the beginning of the breeding season, since the individuals who comprise the population are the survivors of those born during the preceding summer, and thus will be concentrated entirely in the older age classes. To make this imaginary population at all comparable to any which might exist under natural conditions, we ought, therefore, to have begun the breeding with some skew form of age distribution. To test the influence of this factor, another calculation was carried out, starting the laboratory population with 1000 virgin females concentrated in the 32–40 weeks age class. It was assumed that these females were subject to the observed life table as regards their age, but that they would produce daughters with the same maternal frequencies (m_x) as though they had started breeding at the normal laboratory age. This latter assumption appears to be justified, at least approximately, by such observations as we have been able to make both in the laboratory and the field. In all essential respects the final results were similar to those given in Table 9 and Fig. 2; the main difference being that the values of r_a' for a given length of breeding season were found to be a little lower. Principally this was due to a slight initial lag and to the fact that, although the population very quickly approached a Malthusian type of increase and age distribution, the average value of r (0·0829) over a period of 24 weeks was less than that used in the text. By assuming that the stable age distribution is already established, the calculations are greatly simplified, and the main argument

is not materially affected by the consequence that thereby the rate of increase during the breeding season is somewhat exaggerated.

Although this model population has been simplified to an extent which makes it appear almost a caricature of any existing in nature, yet it has served the useful purpose of focusing attention on several points. Of these, the principal appears to be the importance of the observed life table, with the mode of its deaths occurring relatively early in life and a mean expectancy of life at birth of only some 30 weeks. But this raises the question of what accuracy can be attached to it and to what degree of variability it is subject under natural conditions. It is always possible that this life table may be that of the vole under less optimum conditions than have been assumed, or that a considerable degree of heterogeneity in the laboratory population has been concealed by the smallness of the sample. Indeed, it would be surprising if further work does not modify many of the figures which have been given here. But the collection of this type of data is a lengthy, tedious and expensive occupation, and, in the meantime, these possibilities do not detract from the general interest of studying the influence of an intermittent breeding season upon a population with this particular age schedule of mortality. Even though such a population has an inherent power of increase which is relatively very great, it will be extremely susceptible to those changes in its environment which might affect the length and intensity of the breeding season. The crucial section of the yearly cycle, if one section can be called more crucial than any other, appears to be those early weeks of the season which would correspond to the months of March to May or June in the field. For, if in a fluctuating environment a combination of various factors arises, which might lead, either through a lowered birth-rate or an increased death-rate, to the state of affairs represented here as a stationary population, a crash in numbers would seem inevitable. Conversely an early and more prolonged breeding season than the average or a succession of such seasons, coupled with optimum conditions in the environment, could lead to an enormous increase—the so-called vole plague. The general impression left on one's mind is that of a species, which at times will of necessity fluctuate violently in numbers, owing to even comparatively small disturbances of the breeding cycle.

7. Summary

1. The origin of the stock of voles which is bred in this Bureau and the method of keeping them are briefly described.

2. A life table, based on the life-histories of 85 males and 34 females, has been constructed. These 119 individuals were observed from the age of three weeks and their mean length of life was $33{\cdot}94 \pm 1{\cdot}555$ weeks. The probability at birth of dying within the first two weeks of life was estimated as $0{\cdot}13469 \pm 0{\cdot}015423$, and allowing for this degree of infant mortality the expectation of life at birth was found to be 29·7 weeks.

3. The sex ratio at weaning, based on 505 young, was $50{\cdot}89 \pm 2{\cdot}22\,\%$ of males.

4. From the data relating to the 34 females, who passed the whole of their adult lives paired with a male, a table of fertility according to the age of the mother has been formed, giving the mean number of daughters born per eight weeks per female alive during the corresponding eight-week age period.

5. The rate of natural increase has been calculated for a population subject to the observed age-schedules of mortality and fertility, when the appropriate age-distribution has become established. This rate of increase amounts to 87·7 per thousand per week, which corresponds roughly with a power of multiplying some ten times in six months.

6. The influence of an intermittent breeding season of variable length upon the annual rate of increase of such a population is discussed very briefly. Some calculations are given which show, under certain simplifying assumptions. how great the summer increase must be in order to obtain quite a moderate annual increase. Finally, it is suggested that a population subject to this particular life table must of necessity be extremely sensitive to those changes in the environment which might affect the length and intensity of the breeding season.

7. Some additional data, which slightly modify some of the above figures, are given in an addendum.

8. Addendum

Since the above text was completed, some additional data, relating to 13 mated males and 12 mated females, had accumulated. The mean length of life of the males was $262{\cdot}2 \pm 19{\cdot}01$ days and that of the females $263{\cdot}8 \pm 25{\cdot}79$ days; their combined d_x distribution, using the same age intervals as in Table 2, section 3, being

Age in weeks	d_x
19	4
27	6
35	9
43	1
51	4
59	1
Total	25

The 12 females gave birth to 204 live young, of which 165 were still alive at weaning, giving the probability of dying within the first two weeks of life as 0·19118. This may be compared with the original figure, based on 490 live births, of 0·13469. The difference of $0{\cdot}05649 \pm 0{\cdot}029858$ between the two ${}_2q_0$ figures is 1·89 times its standard error and cannot be regarded as significant. The mean infant mortality is thus 0·15130.

It must be admitted that when the figures of the above d_x distribution are added to those of Table 2, the type of equation used in section 3 to smooth the

life table does not give a very satisfactory fit to the combined data, the smoothed l_x graph falling very definitely and consistently below the observed points during the first half of the curve and above during the second half. No further attempt has been made to graduate the combined data; but since the values of P_x are required at the pivotal ages of the fertility table in order to recalculate the value of r, the d_x column was regrouped using different age limits. We give below (Table 10) the final unsmoothed life table based on the life histories of 144 male and female individuals with a mean length of life of $34{\cdot}57 \pm 1{\cdot}343$ weeks. The terminal values of q_x and e_x are worthless and have not been tabulated: but those values of e_x which are given are based on all the data.

Table 10. *Unsmoothed life table*

Based on 144 individuals aged 3 weeks; males and females combined

Age in weeks	Observed				
x	d_x	l_x	$10^5 P_x$	q_x	e_x (weeks)
0	—	—	100,000	0·15130	29·62
2	—	—	84,870	0	32·72
3	5	144	84,870	0·03472	31·72
8	10	139	81,923	0·07194	27·77
16	26	129	76,029	0·20155	21·61
24	26	103	60,706	0·25243	18·06
32	24	77	45,382	0·31169	14·80
40	25	53	31,237	0·47170	11·70
48	15	28	16,502	0·53571	10·57
56	9	13	7,662	0·69231	10·15
64	2	4	2,357	—	—
72	—	2	1,179	—	—
80	1	2	1,179	—	—
88	—	1	589	—	—
96	1	1	589	—	—

The twelve females gave birth to 52 litters containing 204 live young (average 3·92 per litter), and the distribution of the litters grouped according to the age of the mother has been added to those already given in Table 4, section 4, with the result shown in Table 11. A word should be said about the span of the reproductive ages. So far as our observations went, there appeared to be no clearly defined menopause. The oldest female, which lived to the age of 86 weeks, produced her last litter containing live young—her thirteenth

Table 11

Age of mother in weeks	No. of litters containing one or more live young	Total no. of live births	Mean no. of live births per litter
4–	16	52	3·25
12–	63	225	3·58
20–	52	211	4·06
28–	31	116	3·74
36–	19	59	3·10
44–	8	24	3·00
52–	2	4	2·00
60–	0	0	—
68–	1	3	—
Total	192	694	3·61

pregnancy—at the age of 70·6 weeks; but she was later pregnant again and bore one dead embryo during the 77th week of her life. Thus conception is possible up to a relatively very advanced age. It was observed that towards the old age of successful breeders, the interval between pregnancies became longer, the litter size became smaller as indicated in Table 11, and a large proportion of the litters were still-born. If a female survived this stage, there might remain a period of variable length before her death during which no pregnancies were recorded: but more commonly a female would die while she was still apparently fecund.

The table of fertility can now be based on the life histories of 46 females, and the average number of these who were alive during the different eight-week age periods is tabulated below under the heading E_x.

Table 12

Pivotal age in weeks x	E_x	No. of daughters	m_x	P_x	$P_x m_x$
8	45·5	26·0	0·5714	0·81923	0·4681
16	42·5	112·5	2·6470	0·76029	2·0125
24	34·0	105·5	3·1029	0·60706	1·8836
32	25·5	58·0	2·2745	0·45382	1·0322
40	19·0	29·5	1·5526	0·31237	0·4850
48	11·5	12·0	1·0435	0·16502	0·1722
56	5·5	2·0	0·3636	0·07662	0·0279
64	2·0	0	0	0·02357	—
72	1·0	1·5	1·5000	0·01179	0·0177
	Total	347·0			$R_0 = 6·0992$

The values of P_x are taken from the above unsmoothed life table and the sum of the $P_x m_x$ column gives the ratio of 6·0992 between the female births in two successive generations, as compared with a figure of 5·9042 in Table 6, section 5. The value of the rate of natural increase (r), calculated as before to a fourth degree approximation, was found to be 0·09035 and the mean length of a generation 20·01 weeks, figures which show only small differences from those of 0·087703 and 20·25 weeks originally calculated in section 5. This agreement suggests that a recalculation of the birth-rate, death-rate and age distributions, together with the whole of section 6, would have resulted in substantially little difference from those figures already given in the text.

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THE DENSITY OF WOODLAND BIRDS DETERMINED BY THE SAMPLE COUNT METHOD

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1. Introduction

The need for data to illustrate the relative abundance of the species comprising a bird community has been widely recognized for some time. Recently (**5**), it has been stressed that the taking of a complete census may not be justified by the labour involved, and that the essential facts can often be obtained by sampling the bird population. But because of the necessity for a long series of counts, this sampling in itself can be tedious, both in the field and in the working up of a mass of figures, and it has therefore been felt desirable that methods of sectional counting should be kept as simple as possible so that any competent observer could do one during the course of a walk, or while undertaking other observations. It was apparently with these points in mind that Linsdale (**6**, **7**, **8**, **9**) and others have advocated recording the frequency of occurrence of species, which is nothing more than a species list made on each visit to one habitat, ultimately expressed as a percentage:

$$\frac{\text{No. of times species occurred} \times 100}{\text{No. of visits}}.$$

This is undoubtedly the simplest method which could be devised.

Lack's paper (**5**) provides a useful guide to other methods which have been used by various workers. It is unfortunate that the word "census" has been applied indiscriminately to such extremes as the laborious examination of a habitat, yard by yard, and to road counts taken from a relatively fast-moving

car—a method quite without value in wooded country. It is to be hoped that in the future the term will only be used when a careful count has been made of all the birds within the area, with the addition of a knowledge, during the breeding season, of whether birds are paired or unpaired. Confusion between the census or part census (in strip sections or sample areas) and the sectional or sample count would then be eliminated.

A method suitable for open country is not necessarily adaptable to woodlands. The observer is not free to move in a straight line, so that his course can seldom be mapped with accuracy; his view is restricted; he must move quietly and therefore slowly; disturbance is increased with each co-worker, so that the population being sampled is not a natural but an alarmed one. For these and other reasons (including simplicity of measurement) the sampling unit of time is preferred to that of space, although one cannot be entirely divorced from the other unless the plan is adopted of remaining stationary for fixed periods (**12**). But it was felt that here the assumption was made that the habitat, or the distribution of life within it, is more uniform than is actually the case, an objection which is also applicable to the sample census.

In recording specific frequency it has been the practice to use a day as the unit of time, a unit too large, however, for the limited wooded areas of this country. Linsdale states that species recorded after the first four hours are not of much significance, but if by "significance" is meant ecological importance, a four hour unit must be regarded as too high. Dice (**1**) suggests a time unit of half an hour, and there is much to be said for shortening it; but probably the hour would be the most acceptable and is suitable for all but the smallest habitats. When the unit is reduced it becomes necessary to adhere to it more strictly than has been customary. An alternative method of recording frequency, eliminating the need for a large number of visits—Linsdale mentions over a 100—is suggested in this paper.

With all these methods based on time, as indeed with those based on distance, the walking speed of the observer is of importance: the fast walker records more individuals and species in the same time, and less in the same distance. Thus, Winterbottom (**13**) found that only about two-thirds of the total number of species was seen in an hour; but if he had walked slowly over the same course he would presumably have recorded more. The interplay of space and time during comparative counts presents a problem of no little complexity.

The counts which are summarized here were undertaken with the object of ultimate comparison with the known breeding population. Some doubt was felt about methods which took no account of the numbers of individuals, and these were therefore recorded, together with the species encountered and the time involved. Later, the method was tried out on an unknown population, and some tests made at different observing speeds. Finally, the results obtained

seemed to merit a discussion of the methods and those factors affecting them which have hitherto received little attention.

For much helpful criticism and advice, together with reading facilities at the Bureau of Animal Population in Oxford, I am indebted to Mr Charles Elton.

2. Breeding census and counts

(*a*) *Census area.* This was a typical mixed wood on the Berkshire downs, close to the Wiltshire border. Straight Copse stands 650 ft. above sea-level; its area is 11 acres. The district generally is cultivated downland, with other "island" woods; but except on the north it is actually surrounded by grassland, though at the north east corner it is linked to a smaller copse of the same type. There is little old timber, and the oaks (*Quercus robur*), ashes (*Fraxinus excelsior*), with a few other trees, average 21 to the acre. Approximately 17 % of the total area had been coppiced immediately prior to these observations; 18 % had been cut the previous winter, so that the hazel (*Corylus avellana*) stood at about 4 ft.; the remainder, excluding some paths, exceeded 8 ft. in height. Patches of bramble (*Rubus*) and bracken (*Pteridium aquilinum*) provided nesting cover.

(*b*) *Method.* Each bird positively identified by sight or sound was recorded during a timed and dead slow progress through the habitat. An attempt was always made to see a bird which had been identified by sound alone, but if it remained unseen it was only recorded when it could be localized in any one tree or group of shrubs; all distant songs and calls were ignored, but there was no distance limit when identification was visual. Birds flying overhead were similarly ignored unless they were seen to fly out of or into the vegetation. Many birds were passed over because their identification was not certain. No attempt was made to record the maximum number, entries only being made for those identified during general observations on territory and behaviour.

If a stationary period exceeded 5 or 10 min., or if attention was given exclusively to one bird, a note was made of the time involved and such periods were subtracted from the total. Care was taken not to cover the same ground or record the same birds twice. Neither the route traversed nor the time spent in the habitat was constant, but the majority of the counts were made in the early morning, before 8 a.m. Time spent in hunting for nests was not included, the object being to move as quietly as possible, although progress was not confined to paths or tracks; this reduces the observing speed considerably, but a low speed is an advantage in that sufficient time can be spent in small areas (or subareas) to allow them to be sampled.

The counts are expressed as adults recorded per hour, for all species, and per 10 hr. for each species. In later work it was found to be worth a little extra trouble in the field to arrange, whenever possible, for the observation to be in complete hours, or, whenever a series was being taken in any one habitat,

for the sum of the observations to total 10 or 20 hr. Here, however, observations were begun when the habitat was entered and stopped when it was left, a note of the time being made on both occasions. The series was taken in the spring of 1938; 62 observations covering three months, with a total time of 96 hr.

For general record keeping 5 × 3 in. slips were used, together with a system of symbols and letters which obviated the necessity for writing out the names of species. But in Straight Copse, territory was being studied and all birds identified were actually mapped in the position first seen or heard.

(*c*) *Results.* The mean indices (birds per hour) for each month, together with their standard deviation, are given in Table 1. The coefficient of variation

Table 1. *Monthly means and range of the daily adult bird per hour index*

	April	May	June	Total
No. of observations	20	25	17	62
Mean	18·4	22·4	21·7	20·9
Standard deviation	±5·6	±3·0	±5·0	±4·8
Coefficient of variation	30·4	13·4	23·0	23·0

expresses the standard deviation as a percentage of the mean. It will be seen that the index tended to remain fairly constant from day to day. An unusual April minimum occurred on the 2nd, with another low reading on the 3rd, these being days of moderate and strong wind with some drop in temperature, the only days in April when anything above a light wind was recorded. There were also two high readings for the last two days of June, when probably some juveniles were recorded as adults. These readings compared favourably (though they were slightly higher) with those taken in larger woods. There was some suggestion that a rise in temperature caused an increase in the number of birds singing two or three days later, but there was no significant correlation between the index and temperature. The lower mean for April would appear to be due to the migrants not having fully arrived in that month, but when the two days of wind are omitted from the mean it rises to 19·8. The actual rise for May is therefore 2·6: in this month the opening of the foliage, the arrival of the migrants, and full song, all occur together. In June the index shows no appreciable fall, and although care was taken not to include birds of the year, some error is bound to creep in; there may also have been a loosening of territories. While at the beginning of the period nearly all singing birds were seen, the majority remained hidden at the season of full song.

Table 2 shows the species abundance for each month, together with the actual population. As regards the census figures it has been necessary in a few instances, when the territory overlapped the boundary of the area, to count a pair as one bird; but species which obtained their food, or part of it, from outside their breeding territory are included, these being jay, cuckoo,

wood-pigeon, turtle-dove, and the three species of *Turdus*. The resident wood-pigeon population appeared to be constantly changing; in all instances five or more of one species found together were counted as a flock, were entered in the records as "F", and are ignored in the totals. (Over the whole period the wood-pigeon has a value of only 4 F; and the rook of 5 F—in June.) The total census is considerably smaller than the maximum obtained from small mixed copse samples (**5**).

Table 2

	Abundance recorded per 10 hr. (walking counts)				Complete census		Coefficient of conspicuousness
	April	May	June	Av. (3 months)	Actual	Per 100 acres	
Rook (*Corvus frugilegus*)	0·3	—	1·7	0·5	—	—	—
Jay (*Garrulus glandarius*)	2·1	0·8	5·5	2·4	2	18	0·75
Starling (*Sturnus vulgaris*)	—	—	1·7	0·4	—	—	—
Greenfinch (*Chloris chloris*)	0·5	0·3	1·7	0·7	1	9	—
Hawfinch (*Coccothraustes coccothraustes*)	0·3	—	—	0·1	—	—	—
Goldfinch (*Carduelis carduelis*)	—	0·5	—	0·2	—	—	—
House-sparrow (*Passer domesticus*)	1·2	5·4	3·4	3·4	2	18	0·53
Chaffinch (*Fringilla coelebs*)	11·2	16·3	9·8	12·9	10	91	0·71
Bullfinch (*Pyrrhula pyrrhula*)	5·3	4·4	3·8	4·6	4	36	0·78
Yellow bunting (*Emberiza citrinella*)	0·3	—	0·4	0·2	—	—	—
Tree-creeper (*Certhia familiaris*)	0·3	0·5	1·3	0·6	1	9	—
Nuthatch (*Sitta europaea*)	0·3	—	1·7	0·5	1	9	—
Goldcrest (*Regulus regulus*)	—	0·5	—	0·2	—	—	—
Great-tit (*Parus major*)	6·8	4·9	4·3	5·4	3	27	0·50
Coal-tit (*Parus ater*)	—	—	1·7	0·4	—	—	—
Marsh-tit (*Parus palustris*)	3·0	2·3	8·1	4·0	2	18	0·45
Blue-tit (*Parus caeruleus*)	9·5	5·7	6·4	7·2	4	36	0·50
Long-tailed tit (*Aegithalos caudatus*)	4·7	4·4	4·3	4·5	4	36	0·80
Spotted flycatcher (*Muscicapa striata*)	—	1·1	0·4	0·8*	1	9	—
Whitethroat (*Sylvia communis*)	—	5·7	1·3	4·0*	4	36	0·90*
Garden warbler (*Sylvia borin*)	—	3·9	6·0	4·6*	2	18	0·39*
Blackcap (*Sylvia atricapilla*)	3·3	7·0	11·9	8·8*	4	36	0·40*
Willow-warbler (*Phylloscopus trochilus*)	13·3	24·3	23·9	24·0*	9	82	0·34*
Chiffchaff (*Phylloscopus collybita*)	10·4	5·7	6·4	7·5	2	18	0·24
Mistle-thrush (*Turdus viscivorus*)	4·7	0·3	0·9	2·0	2	18	0·90
Song-thrush (*Turdus ericetorum*)	27·2	26·8	15·8	24·2	12	109	0·45
Blackbird (*Turdus merula*)	23·4	42·3	33·7	33·5	16	146	0·44
Robin (*Erithacus rubecula*)	15·4	14·2	6·0	12·6	8	73	0·58
Nightingale (*Luscinia megarhyncha*)	—	9·6	8·5	8·5*	4	36	0·42*
Hedge sparrow (*Prunella modularis*)	11·2	7·2	2·1	7·4	7	64	0·87
Wren (*Troglodytes troglodytes*)	7·7	4·4	4·3	5·5	5	46	0·84
Cuckoo (*Cuculus canorus*)	0·3	3·4	3·0	3·2*	1	9	(0·28)*
Wood-pigeon (*Columba palumbus*)	18·9	18·1	29·8	21·2	7	64	0·30 (0·35†)
Turtle-dove (*Streptopelia turtur*)	—	3·6	8·1	5·3*	4	36	0·68*
Pheasant (*Phasianus colchicus*)	3·0	0·3	0·4	1·2	1	9	—
Partridge (*Perdix perdix*)	—	0·5	—	0·2	—	—	—
					123	1116	

* Omitting April. † Omitting June.

(*d*) *Conspicuousness.* It will be seen that the 10 hr. unit gives results often comparable with the actual population, except for certain dominant species—compare, for instance, the figures for the bullfinch or long-tailed tit. It happens that these two species are of about equal conspicuousness in the field, both vocally and visually. When the values in each column differ widely, as in the case of the willow-warbler, whose abundance is nearly three times

that of the census figure, it is due to a change in conspicuousness—in this instance song. When, therefore, the abundance recorded per hour (y) and the adult population per acre (P) are known, a coefficient or relative conspicuousness (c) for each species can be obtained from the formula

$$c = \frac{P}{y},$$

which is a correction coefficient for differences in voice or behaviour. Thus, in the calculated values of c given in Table 2, while great- and blue-tits are equal, the marsh-tit has a slightly lower value, presumably due to its well-known habit of feeding in the shrub stratum and therefore being more conspicuous. It is obvious that the singing warblers will have a very low coefficient, while silent retiring species will yield the highest value.

Some species present difficulties; thus the mistle-thrush has reared its brood and left the habitat before others have started breeding. There is here a change in habitat which would alter the value of the coefficient. The jay shows a change in behaviour, managing to be extraordinarily secretive until the young are out of the nest, and then being much in evidence as the young fill the wood with their uproar. With this species it would be inadvisable to calculate the coefficient from the May abundance alone, as might be advantageous with some others: certainly in June there are signs of the beginning of a general breakdown in population stability. These difficulties could be overcome by a different coefficient for each month, but (although these can be obtained from the data given) the coefficients in Table 2 cover, with certain necessary exceptions, the three-month period.

The most conspicuous species proves to be (as might be expected) the chiffchaff, but actually the coefficient value is a little too low, owing to an extra pair being present for the first half of April until they were driven out by a wave of willow-warblers. It is $3\frac{3}{4}$ times as conspicuous as the most secretive species. Besides the mistle-thrush, the whitethroat has a high coefficient, song ceasing earlier in the season than usual (the spring of 1938 was notable for precipitation being under normal). Another species with high coefficient, the hedge-sparrow, would have a very different value earlier in the season, especially March, when it can be observed without difficulty.

It must be emphasized that the coefficients here presented are only tentative, for a series would have to be obtained by different workers under varying conditions before they can be regarded as anything else. With this reservation, it seems possible that when c and y are known, and also the area being sampled, it should be possible to estimate P with a fair degree of accuracy. The ratio y to P for all species may be regarded as the coefficient of the habitat, and it would be interesting to know how this varied from one area to another. In the present instance the habitat coefficient of conspicuousness is 0·53.

Frequency occurrence of species did not give an accurate estimate of the first six species; thus the wood-pigeon and blackbird together ranked first, song-thrush second, the conspicuous chiffchaff third, then chaffinch and willow-warbler fourth, followed by robin, blackcap, blue-tit, nightingale, wren. The chiffchaff of course holds this position by the persistency of its song, as to a lesser extent does the blackcap; while the wood-pigeon owes it to its bulk and clumsy flight through the woodland. If the conspicuous species rank too high in a series of 62 observations they would presumably still do so with a larger number; while the fact that a 90 min. time unit was only approximately adhered to should not affect the relative order of the dominant species. Even if vocal identification alone were disallowed there would still be a wide range of conspicuousness; but to ignore an identified bird which, although within a few yards, remained hidden by some freak of foliage, would probably seem unreasonable to the majority of observers. When individuals have been counted, a correcting coefficient can be applied.

(*e*) *Further analyses.* Using the hour as the equivalent of a quadrat, an index number of the frequency abundance for each species, such as has been used in botanical work (**11**), was calculated; but a welter of computation disclosed no advantage over the abundance figures here given.

Out of the whole series of readings a sample was taken at ten period intervals, with a slight adjustment of one in order to make the total time of the sample exactly 10 hr. (and so facilitate calculations). While not giving such a reliable result as a 20 hr. sample, which closely approached the mean for the whole period, the 10 hr. sample presented a more accurate picture of relative abundance than that given by frequency percentage obtained from a total period of 96 hr. It is concluded that samples should (in summer) exceed 10 hr. (or 15 hr. when special specific accuracy is required); when this is followed, and no single observation is much less than an hour, specific abundance value of 10 or over (1 per hour or, in the present habitat, approximately one adult to two acres) denotes dominance. The hourly index for the 10 hr. sample was 21·7 birds per hour, and, using the habitat coefficient, the calculated population $21{\cdot}7 \times 0{\cdot}53 \times 11 = 126{\cdot}6$, which when compared with the actual population shows an error of only 2%.

3. Counts in Savernake Forest (Wiltshire)

(*a*) *Winter counts.* Although the number of observing hours necessary to obtain accuracy is probably less during winter, because of the absence of foliage, the sampling of populations is of less value in small areas for two reasons: first, the habitat being small and birds more prone to movement, there is a danger of recording the same birds twice; secondly, fluctuations in the winter bird population of an "island" copse vary from month to month, day to day, and even day to night. Any winter estimate or census figure

would have to be an arbitrary one, and would seem to have little value unless it also embraced the surrounding country.

Savernake Forest represents this country in the lack of uniformity common to deciduous areas. The Forest can be classified into at least four main groups, often with patchy distribution. Thus the fairly dense stands of beech (*Fagus sylvaticus*), with no scrub, occur in circular clumps and long avenues, with an intervening vegetation of quite a different type. Into the oak (*Quercus robur*) and bracken (*Pteridium aquilinum*) which predominates, has crept hawthorn scrub (*Crateagus*) in so uneven a manner that it becomes difficult to separate the two types; yet it is believed that the presence or absence of that scrub may be a deciding factor in the distribution of forest birds. The walks on which the present counts were recorded, however, took no note of this problem and treated the Forest as a unit.

The counts of the most important species, reduced to the 10 hr. unit, appear in Table 3, the method being the same as that used in Straight Copse. The first column gives the results of recordings taken in October, November and January, and although the dates are rather widely spaced there were only two marked specific fluctuations. One of these naturally concerns the wood-pigeons, which descend in uncountable numbers on to the acorn crop; the figure for this species only takes into account stray individuals, ignoring the 20 flocks also counted, and does not indicate the overwhelming dominance over all other species. The numbers of wood-pigeons were very great at the end of October, but the peak was reached in the first half of November. By the end of the month there were only half as many, while in January and February only half a dozen birds were seen. The second and less important fluctuation was an influx of blackbirds at the end of November, three times the normal number being recorded; this has the effect of giving the species a high position in rank. The total for all species excluding the wood-pigeon was 17·3 birds per hour.

(*b*) *Comparative counts at different observing speeds.* It became apparent that the influx of summer migrants is cancelled out by the opening of the foliage, in spite of the ease by which many migrants can be vocally identified. But it was felt that the normal observing speed was greater in winter than in summer, and it seemed desirable to find out what effect an increased speed would have on the number of birds recorded. With this object a course through the Forest was chosen which could easily be measured on the 6 in. map, and was traversed ten times in the latter half of February, when birds were mostly paired but still in flocks. The course was 2 miles 25 chains (2·31 miles). On the first day's observation the course was covered at a fairly brisk walk, the return journey being slow enough to occupy double the time, this being the normal winter counting speed; on the next day the slow journey was made first, and so on, with the object of smoothing out any differences due to time of day—though all counts were made between 9 a.m. and 2 p.m. Each course was timed,

Table 3. *Savernake Forest*, 1938–9. *Abundance recorded, "Timed frequency occurrence" of species and comparative ranking, at different observing speeds, for the ten most abundant species.* (*Order of rank in brackets*)

	Abundance recorded per 10 hr. at different speeds			"Timed frequency" (mean no. of minutes until species is encountered)		Abundance recorded per 10 hr. at different speeds	
	Oct., Nov. and Jan. 1938	Last two weeks in February 1939			Mid-June 1939		
	1–1·25 m.p.h.	1·05 m.p.h.	2·46 m.p.h.	(Mean 1·47 m.p.h.)	(Mean 1·47 m.p.h.)	1·09 m.p.h.	2·27 m.p.h.
Carrion crow	1·8	0·9	—	95	43 (10)	3·8	13·8 (8)
Jackdaw	F	F	6·4 F	65	29 (4)	15·9 (5)	29·5 (5)
Jay	8·9 (7)	5·4	12·7 (7)	60	88	0·9	—
Starling	—	1·8	—	72	44	4·7	17·7 (6)
Chaffinch	4·5	2·7	10·6 (8)	53 (8)	11 (1)	31·9 (1)	35·4 (3)
Tree-creeper	2·7	11·8 (8)	10·6 (8)	44 (6)	92	1·9	—
Nuthatch	12·5 (5)	13·6 (6)	14·8 (6)	38 (5)	41 (9)	7·5 (7)	9·8
Great-tit	16·2 (3)	27·2 (2)	64·7 (1)	27 (4)	48	11·3 (6)	5·9
Blue-tit	16·2 (3)	14·5 (5)	23·3 (4)	44 (6)	35 (6)	7·5 (7)	11·8
Coal-tit	7·3	10·0 (9)	23·3 (4)	55	58	3·8	5·9
Marsh-tit	14·2 (4)	30·0 (1)	31·8 (3)	23 (1)	63	3·8	5·9
Goldcrest	8·9 (7)	—	—	—	—	—	—
Willow-warbler	—	—	—	—	30 (5)	16·9 (4)	31·5 (4)
Mistle-thrush	0·9	10·0 (9)	10·6 (8)	50 (7)	40 (8)	3·8	5·9
Blackbird	32·9 (2)	20·8 (3)	42·4 (2)	25 (3)	12 (2)	15·9	29·5 (5)
Robin	16·2 (3)	15·4 (4)	17·0 (5)	24 (2)	47	7·5 (7)	15·8 (7)
Redstart	—	—	—	—	16 (3)	24·4 (2)	37·4 (2)
Wren	9·8 (6)	12·7 (7)	31·8 (3)	44 (6)	56	6·6 (8)	11·8
Green woodpecker	3·6	4·5	8·5	63	59	4·7	13·8 (8)
Wood-pigeon	43·6 (1)	5·4	4·2	77	36 (7)	20·6 (3)	43·3 (1)
All species per hr.	21·6	19·9	33·8	—	—	21·3	36·0
Standard deviation	±3·6	±3·0	±8·2	—	—	±1·7	±3·2
Coefficient of variation	16·7	15·1	24·3	—	—	8·0	8·9
No. of species	20	23	20	24	34	29	26
No. of times course covered (2·31 miles)	—	5	5	10	10	5	5
Time spent, hr.	11·25	11·03	4·70	15·73	15·75	10·67	5·08
Adults per mile	Not known	19·0	13·8	—	—	19·7	15·8
Adults per km.	Not known	11·8	8·6	—	—	12·3	9·9

the counts being finally added together to form two groups, fast and slow; the figures for the ten most abundant species appear in the second and third columns of the table. It will be seen that the fast-slow ratio was 2·3 to 1 in speed of walking, 1·7 to 1 for birds recorded per hour, and 0·7 to 1 for birds recorded per mile. The number recorded per mile was practically the same as that recorded per hour because the pace averaged about 1 m.p.h.

It was hoped that the course would be characteristic of the Forest vegetation as a whole, but it was soon seen that the more open areas with considerable thorn scrub were over represented at the expense of denser stands of oak with only bracken. This is reflected in the bird per hour index, which is too high for the whole Forest. Work done so far indicates that there is a summer increase of 2 birds per hour at the eastern end of the Forest as compared with the western end (oak and bracken); but it is not yet possible to say whether the distribution of species is involved. It is necessary to remember that the

index in the first column included the wood-pigeon. But even bearing in mind this lack of uniformity, some of the differences between the first two columns are so great as to suggest that there was a February influx of tree-creepers, marsh-tits and great-tits, but not of nuthatches or blue-tits. The mistle-thrush is well known to feed in open country during most of the winter.

It is believed that the second column gives an accurate picture of the relative abundance of these species during the latter half of February. The counts for the quicker rate of walking are given for comparison only: this speed is not advocated for woodland. It demands a track or path, a high degree of concentration, and is apt to give too high a place to those birds making the most noise on being disturbed.

In these winter counts the same method of not attempting to count flocks, but simply recording them, was used. This has the effect of concentrating on the more residential birds, the loosely integrated nuthatch-titmouse flocks being regarded as individuals. Numbers not included in the counts of Table 3, were, besides wood-pigeons, a few flocks of chaffinches, rooks and jackdaws (*Corvus monedula*). Only the latter, with a decided preference for old timber, should be included among the most important species.

In the middle of June a further series of counts was recorded over the same fixed course, at approximately the same two speeds. The recorded abundance is included in Table 3, for comparison with the winter counts. The hourly index is only 1·4 (adults per hour) higher than in winter, at the slow speed, with the index at the quicker rate varying proportionately. (It must again be emphasized that the course was not representative of the Forest; the extent of the *Crataegus* scrub is indicated by the willow-warbler ranking fourth.) The ratios between individuals and species at the different speeds are similar to those already discussed, but the standard deviation is lower than in the winter counts, when birds were presumably less sedentary. It is worth remarking that the coefficient of variation, both summer and winter, is lower for the slowest observing speed, while there is again some indication that conspicuous species rank too highly when the speed is increased. But there will always be some variation in relative conspicuousness, whatever the observing speed. Within a limited area, the redstart (*Phoenicurus phoenicurus*) is a decidedly conspicuous Passerine, both in coloration and persistency of song, and although it is a notable summer bird of the Forest it would probably rank too high in any system of sampling, unless due allowance had been made for this factor.

(*c*) *Timed frequency of occurrence of species.* The middle columns of Table 3 were obtained by setting a watch at zero (any hour) at the start of observations and then recording the minutes past the hour when the species was first seen or heard (close at hand). Finally, the sum of the minutes for each species was divided by the number of visits, and the species then appear in order of their relative abundance. To correct a species having a value of 0 when it was not

recorded at all, and therefore being ranked too high, such blanks were filled up by the total number of minutes of the observation. Records are simple to keep, and as an alternative to the more usual method of stating the frequency of occurrence of species it would seem to give as accurate an order of rank in (say) a tenth of the number of visits. Observations may occupy 1–2 hr., but an agreed time unit becomes unnecessary since it is a component of the method itself.

(*d*) *Conspicuousness in open country*. Some of the larger conspicuous birds, such as the crow (*Corvus corone*) and green woodpecker (*Picus viridis*), occurred in open parkland (of which there are stretches in the Forest), where they were visible over a long distance. This opens a problem which, while not associated with sampling in woodland, where troubles are mainly due to concealing adaptations, has certainly not received adequate attention. As soon as the wood becomes so open that the habitat itself no longer provides a close limitation to visibility, relative specific conspicuousness varies probably more widely than in woodland. For example, if an observer walks for one mile over flat marshland, where the vegetation consists of coarse grass, reeds or small *Salix* withy beds, the conspicuousness range (area over which a species can be identified) of a lapwing (*Vanellus*) would be 640 acres, and that of a reed bunting (*Emberiza*) 73 acres, allowing as normal recognition distances half a mile for the former and one hundred yards for the latter. The position is made worse by the larger birds being more easily disturbed over a wide area, while the smaller ones are indifferent unless approached closely. Although counts undertaken in such open habitats, disregarding any variation in specific conspicuousness, may be useful for comparative purposes, they do not, and cannot, yield an accurate account of the bird population. There are two ways out of this dilemma. One is to ignore all birds beyond an imaginary distance limit, with all its attendant difficulties of estimating distances both in the air and over featureless country. The second, and it is suggested that this is the most practical, is to gain some knowledge of the relative conspicuousness of the birds comprising each community.

4. Discussion

The unit of time has been preferred by Grinnell and his co-workers (**2, 3**), who also advocated the recording of individuals. They give many of their "censuses" in full, but although times and approximate distances are published, they have failed to bring their results to a common level so that they can be compared. The most important difference between their method and the one used in this study is that one of their cross country walks may include, for instance, both dense forest and grassy plain. In counting, they recorded as much as they could of a flock and then used a plus sign; uncertain species were entered with a query, or as belonging to a group—as "hawk". Taking the later work (**3**) it appears that their walking speed varied from 0·5 to

3·0 m.p.h. (mean 1·5) and the number of individuals recorded per hour from 4 to 100 (mean 48). That the variation is due to diversity of habitat is suggested by one count, where 123 birds were recorded in 4·8 hr., 119 of these being seen in the first 2 hr., when the observer was passing through woodland. In another place (**8**) Linsdale stresses the need for uniformity of habitat. From October counts in Rhodesian woodland Winterbottom (**13**) obtained 77 per hour at a mean speed of 4 m.p.h.; but the total time involved was only 3·75 hr.; he was using a short distance limit and probably did not attempt to use field glasses, but even then his speed is high.

Hicks & Chapman (**4**) tabulate figures of an organized winter census in which nearly a quarter of a million individuals have been recorded, and give comparative rankings based on the number of individuals and species frequency. The mean number of individuals per census (day) was 569, but a similar census in Indiana (34,299 individuals) was less than half that number; again, all types of habitat are included. These authors list some of the factors which operate to make one species more conspicuous than another, and state their opinion that gregarious species give the impression of being more abundant than they really are, since 17 out of the first 25 species in order of counts of individuals were of flocking habit, while, when the ranking was by the number of times the species was reported, there were only 10 of flocking type. This evidence does not seem to be conclusive, as other factors may have been at work. Moreover, the density of the vegetation has to be taken into account; for example, it is only possible to get down on paper a very small proportion of a nuthatch-titmouse flock, owing to the difficulties of sorting out the species and to losing touch with those which have already been counted. The degree of probability of an observer meeting different numbers according to whether birds are dispersed or aggregated seems to call for mathematical treatment. Generally, forest birds on the British list do not present much of a problem in this respect.

Sufficient data have been given to show that the walking speed of the observer is an important factor whenever it is desired to compare populations. It is no less important for counts of species; thus, in the Savernake counts 12–15 % more species were recorded (winter and summer) when the walking speed was reduced. When the time was constant (56 min.), but not the distance, the mean number of species recorded for the five slow winter walks was 9, and for the fast, 13. Moreover, the speed of the observer is directly proportional to the abundance of birds, and inversely proportional to the abundance of vegetation. The former must be so even if he pauses no longer than to identify and record. The theoretical result is that if birds are scarce, the observer's speed tends to increase and he begins to record more (when he is using the time unit, or less for the distance unit); but this source of error is more alarming on paper than in the field, and in practice few birds give a low index value.

In the present study the walking speed during the breeding season is estimated (from measurement on the 25 in. map) as 0·3–0·4 m.p.h. but in woodland where undergrowth was absent, the speed was doubled; in winter it was 1–1·25 m.p.h. Experience has suggested 0·5 m.p.h. to be a useful speed (both summer and winter) at which to aim, but to avoid tedium 1·0 m.p.h. is recommended whenever shrub growth is lacking. An observer's pace is easily tried out over a measured course, and it is desirable that it should be recorded from time to time on all counts of birds, by whatever method. When this is done there seems no reason why the number of birds identified per hour should not be a useful and convenient index which could be used by different workers for expressing the bird populations of woodlands at the same, and ultimately (as data accumulates) at different seasons. It must not be forgotten that the more strictly social species, together with those nocturnally active, call for slightly different treatment (i.e. a census).

Weather conditions affect the readings in two ways; actual abundance of birds, and their conspicuousness. Counts should obviously not be attempted in mist or heavy rain, when binoculars cannot be used. Winter sunlight is a very real advantage in open woodland but loses its value when the view becomes restricted and in the early morning can be a hindrance because of its low angle. A high wind masks both movement and sound and is a decided disadvantage; extraneous noises (aircraft) are a real nuisance. It is generally recognized that the activity of birds varies at different hours of the day (**2**), and the standard time for taking counts is in the early morning during the breeding season and throughout the morning in winter, although variation in the short winter days is probably much less. When birds have once settled to breed, widespread movement presumably ceases and they remain in their territories, and at this time the only known factor (apart from the seasonal one) affecting their conspicuousness as a whole is the influence of temperature on song.

Widespread movements in the non-breeding season, although they may render a count or census of very little value, do not come within the scope of this discussion. But movement within the area being sampled may be a cause of inaccuracy. The February counts here given were taken on five mornings within a fortnight, a high or low reading at one speed being in each instance followed by a corresponding high or low reading at the other. Three mornings at the quicker observing speed gave remarkably uniform results (33·0, 33·8, 33·8 birds per hour), these being mornings of sun, light breeze, and normal temperature. At intervening dates came the extremes: the lowest on a dull day with slight drizzle following a frost, the highest on a sunny morning with dropping breeze following an all-night strong (southerly) wind. The low index was hardly caused by reduced visibility alone, but it is believed that the abundance indicated on the other day was directly due to the wind, the greater part of the course being sheltered by the slope of the hill.

The species most active in their local movements and less tied to any fixed base are the titmouse flocks, and it is therefore suggestive to find that on the day when the highest total (45·0) was recorded the number of great and blue tits was more than double that recorded on any of the other four days, and that these two species (except perhaps the tree-creeper) were the only ones that showed any increase. This walk was taken before the slow one, whose index varied less from the mean with no species having an obviously high value. Whenever Straight Copse is exposed to a high wind a low index is to be expected, this appearing, as has been seen, even so late in the breeding season as April. A correlation between wind velocity and the number of winter residents present in a small area was found by Shaver (**10**). As a factor causing movement, wind has probably been underestimated; it certainly encourages aggregating in the sheltered part of a habitat and perhaps movement from small to large areas. Sampling should not therefore be undertaken when there has been a high wind within the previous 24 hr.

In comparing the various methods to which reference has been made it would appear that they fall into grades, each with a slightly different purpose in view. Grinnell & Storer's sectional counts seem best adapted for comparatively unexplored country. The frequency of occurrence of species as used by Linsdale is an advance on this in that uniformity of habitat is insisted on, but it makes some sacrifice to simplicity of technique. Used on a wide scale, not necessarily by experienced ornithologists, it might be of great value for comparing bird communities. If the suggested modification ("timed frequency") should stand the trial of experience, it ought to be possible to take the measure of an area in so short a time as one week. The number of observations required by the original method is a serious disadvantage. But when our knowledge of bird distribution has reached a fairly high level and the time has come to consider more intensive studies of bird populations, then the recording of individuals becomes an essential. Only by so doing can we have any knowledge of temporary or local fluctuations due to environmental causes, biological or physical—as in the example given.

The area in which this preliminary work was undertaken is admittedly small, but in view of the thick undergrowth it was as much as could be conveniently handled by one person within a limited time. There is considerable scope for team work on this subject, observers doing sample counting individually but combining over the census.

5. Summary

1. The distinction between a census and a count has not always been appreciated, and a more cautious use of the former term seems desirable.

2. In sampling woodlands the unit of time is preferred to that of space, together with a slow observing speed and a random rather than a fixed course.

3. Using this method, a series of almost daily counts of individuals was taken in a small mixed copse throughout a breeding season, the results being expressed as the number of adults recorded per 10 hr., or as a bird (adults) per hour index for all species. A census was taken at the same time and the figures are tabulated together for comparison.

4. A formula is given from which a coefficient of conspicuousness for each species can be obtained, and tentative coefficients are given for those species which bred within the area. When the coefficient is known the computing of populations from sample counts should prove possible.

5. Out of a series of counts in Savernake Forest abundance data are given for the first ten species.

6. The speed of the observer in all sampling methods is of sufficient importance to make it desirable that it should be periodically recorded. It was found that when the speed varied from 2·3 to 1 m.p.h., adults recorded per hour varied from 1·7 to 1, and species per hour from 1·4 to 1.

7. It is believed that wind is an important factor causing local movement, except for a short time when the individual bird's attachment to one spot is very pronounced.

8. The usual percentage frequency of occurrence of species obtained from 62 observations throughout the breeding period compared unfavourably with the census figures, conspicuous species being ranked too high. A method of timing the frequency is suggested, enabling the number of observations to be reduced. But the recording of individuals is essential for an intensive study.

9. More knowledge is desirable on relative conspicuousness in each bird community.

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BIRD POPULATION STUDIES. THE AVIFAUNA OF FORT JAMESON, NORTHERN RHODESIA, 1935–38

By J. M. WINTERBOTTOM

1. Introduction

The present paper deals with a further investigation, from December 1935 to July 1938, by the methods used during the period 1932–5 (of which I have previously given an account (**5**)) of the avifauna of Fort Jameson township. A description of the terrain was given in that paper and, except that an additional station in the extreme south-west corner of the area was added to those used in compiling the "sample counts", I have no field data to add to what was there said. As these methods have now been used by me for investigating the avifaunae of two localities in detail and of others for more limited periods or in a modified form, and since they have recently been the subject of criticism (**3**), I propose to consider briefly what may be learned from these studies and what is their value. Some of these points were touched upon in my account of the birds of Mazabuka (**4**), but a summary, in the light of six years' further experience with them, may be useful.

The various methods of censusing birds may give a fairly accurate picture of the absolute number of birds in a given area at the time of the census, as with the method of direct counts, of which there are few examples for Africa (**2, 6**). Or they may give a less exact but more extended picture, which while providing no absolute figures and not enabling one to estimate the population per acre, may nevertheless throw light on seasonal fluctuations and enable one to compare the avifauna of one locality with that of another, either as regards total populations or in respect of individual species or both. The present methods give no indication of absolute densities. When used to compare the relative abundance of one species with another, they are liable to inaccuracy from two causes: (1) some species are more conspicuous than others; (2) certain species are habitually found in flocks, and the methods adopted are incapable of distinguishing between solitary and gregarious species.

The first of these two points is one that affects all censuses, even the complete count. I do not think it a very serious source of error in the present methods, though it undoubtedly does tend to tilt the beam against inconspicuous species and this must be borne in mind in considering the figures. In order to counteract this as far as possible the areas used for the sample counts were smaller in places where visibility was poor than in places where it was extensive. In general, a radius of 10–20 yd. was used for such counts.

The second point is also a valid criticism; it is to some extent offset by the fact that such species as white-eyes (*Zosterops senegalensis anderssoni*), in themselves inconspicuous, become much less so in flocks, by reason of their numbers and calls. Nevertheless, it is probable that the numbers for this species, for the bee-eaters (*Merops*), some of the swallows (*Hirundo*) and certain other forms are too small as compared with solitary forms. It is, however, true to say that few of the more numerous species are entirely solitary in habit; the bulbul (*Pycnonotus tricolor*) commonly occurs in parties, as do all the weaver family; the wagtail (*Motacilla aguimp*) in pairs and family parties; and the doves, if not strictly gregarious, seem to be often neighbourly. (*Streptopelia capicola* and *S. semitorquata* do flock at times, but I have not noted this habit to any degree at Fort Jameson, though it is conspicuous in other parts of the district, especially at midday and in tall trees near water in the dry season.)

Summing up, we may say that the methods employed in these studies give: (1) reliable data for comparison between the relative abundance of individual species in different places and in different years, (2) somewhat less reliable data for comparison of the relative abundance of individual species at different seasons, the reliability varying with the species (*Pycnonotus*, *Streptopelia*, *Motacilla*, *Uraeginthus*, for instance, being quite reliable, *Cossypha*, *Tchagra*, *Prinia*, less so), (3) an index of the relative abundance of one species as compared with another, subject to the provisos noted above.

There remains the assessment of the relative values of the two methods. For common species, occurring in 80 % or more of the daily lists, the sample counts are undoubtedly more reliable; but for other species, these counts are of less value, since the number of times they occur is so small that the margin of error is disproportionately big. The distribution of the counts by months is shown in Table 1.

Table 1. *Distribution of sample counts and daily lists by months*

	1932–5		1935		1936		1937		1938		Totals	
Month	D.L.	S.C.	D.L.	S.C.	D.L.	S.C.	D.L.	S.C.	D.L.	S.C.	D.L.	S.C.
Jan.	82	203	—	—	28	119	21	78	29	100	160	500
Feb.	70	181	—	—	23	91	8	21	13	33	114	326
Mar.	65	190	—	—	28	100	2	—	29	100	124	390
Apr.	14	44	—	—	18	59	17	53	9	30	58	186
May	48	117	—	—	23	47	31	103	17	44	119	311
June	17	32	—	—	13	23	30	91	6	20	66	166
July	62	100	—	—	20	60	30	78	30	137	142	375
Aug.	32	106	—	—	—	—	—	—	—	—	32	106
Sept.	63	121	—	—	15	61	22	60	—	—	100	242
Oct.	57	153	—	—	6	29	17	40	—	—	80	222
Nov.	60	170	—	—	21	60	13	27	—	—	94	257
Dec.	60	134	27	112	19	73	31	121	—	—	137	440
Totals	630	1551	27	112	214	722	222	672	133	464	1226	3521

2. Daily lists of species

Daily lists of species were kept for 596 days, as against 635 during the previous period. The total number of different forms recorded was 163: 20 more than in 1932–5. Of the latter, 12 were not recorded during the second period, so that the total number of forms recorded from the township by me between July 1932 and July 1938 is 175. The total number of forms admitted by me in the "Revised Check List of the Birds of Northern Rhodesia" (in the Press) is 678.

If the 163 species are divided into groups on the basis of occurrence, such that Group A comprises species occurring in 1–20% of the counts, B in 21–40%, C in 41–60%, D in 61–80% and E in over 80%, we find the following:

Table 2. *Daily lists: Raunkiaer groups*

Period	A	B	C	D	E
1935–8	112	17	10	7	14
1932–5	73	6	9	4	9
1932–8	131	16	8	7	13

It has been found by Raunkiaer, the originator of these groups, that for plants, the formula $A > B > C \gtrless D < E$ holds. Linsdale (**1**) has confirmed this for American birds, but my results for Mazabuka (**4**) and Fort Jameson (**5**) showed irregularities. The present set of results, however, agrees with the formula and so do the combined results for the whole period at Fort Jameson.

In Table 3, I give the seasonal percentage occurrences of the same 37 species as were recorded in Table 4 of my previous paper. These will be referred to again in dealing with individual species.

The average number of species seen per day was 32·5: 4·5 more than in the previous period; this was probably due to increased familiarity with the birds. The highest average for any one month was 41·6 for January 1937; and the lowest 19·5 for June 1938 (only 6 days). The best month, on the average, is December (39·3), when the southern passage is in full swing, followed by January and then March, which I had previously found to be the month most productive of variety. These figures are summarized in Tables 4 and 5, the latter of which shows seasonal averages and brings out that in the wet season about ten more species are seen daily than during the dry weather.

3. Sample counts

For these, ten stations were used. The distribution of counts per month is shown in Table 1. In all, 1970 counts were made, as against 1551 during the previous period. Three months (August 1936, 1937 and March 1937) were blanks, owing to my absence from the township; and in ten further months, the number of counts was less than 50 in each. I have therefore used these figures seasonally only, taking November to April inclusive as the rains and

Table 3. *Daily lists: seasonal percentage occurrences of conspicuous species*

Species	Wet, 1935–6	Dry, 1936	Wet, 1936–7	Dry, 1937	Wet, 1937–8	Dry, 1938
Batis m. molitor	94	70	85	72	88	77
Chalcomitra senegalensis gutturalis	99	99	97	97	94	100
Cinnyricinclus leucogaster verreauxi	35	16	38	18	44	0
Corvus albus	23	45	17	16	27	26
Cossypha heuglini subrufescens	97	94	92	95	95	94
Dicrurus a. adsimilis	94	95	92	95	95	94
Dryoscopus cubla hamatus	94	90	82	88	81	70
Euplectes a. ardens	54	8	34	24	49	11
Euplectes capensis sabinjo	23	1	18	8	11	0
Euplectes h. hordeacea	35	9	40	2	40	23
Hirundo r. rustica	69	9	65	3	68	0
Hirundo s. smithii	67	61	78	52	61	59
Laniarius ferrugineus mossambicus	100	99	95	98	98	94
Lybius t. torquatus	95	82	94	93	93	81
Merops apiaster	79	71*	49	59*	60	—
Motacilla aguimp vidua	100	100	100	100	100	100
Muscicapa striata	65	0	64	0	56	0
Oriolus monacha larvatus	89	96	73	93	40	96
Passer griseus ugandae	97	39	94	81	87	74
Petronia superciliaris	69	66	18	46	62	58
Ploceus velatus tahatali	90	23	74	26	54	38
Pogoniulus chrysoconus extoni	94	84	91	78	81	68
Prinia mistacea graueri	100	45	92	61	91	53
Pycnonotus tricolor layardi	100	100	99	100	100	100
Serinus m. mozambicus	81	65	74	76	65	66
Spermestes cucullatus scutatus	98	83	89	75	98	70
Stigmatopeia s. senegalensis	48	56	55	58	41	87
Streptopelia capicola tropica	100	97	95	95	94	96
Streptopelia s. semitorquata	44	36	41	25	27	51
Tchagra senegala mozambica	94	38	63	38	76	23
Tchitrea perspicillata plumbeiceps†	72	19	73	12	81	—
Turacus schalowi marungensis	77	27	65	7	55	11
Turdus libonyanus niassae	72	73	91	98	92	92
Turtur afer kilimensis‡	100	65	87	56	78	21
Uraeginthus angolensis niassensis	100	99	98	98	97	92
Vinago delalandei	32	22	23	25	29	22
Zosterops senegalensis anderssoni	98	78	75	40	91	70
Number of counts	124	77	88	130	124	53

* Last two months only.

† Present only from the third week in September to the third week in March.

‡ Includes *T. c. chalcospilos.*

Table 4. *Daily lists: species per day per month*

	1935		1936		1937		1938	
Month	Days	Average	Days	Average	Days	Average	Days	Average
Jan.	—	—	28	39·0	21	41·6	29	35·6
Feb.	—	—	23	37·0	8	30·6	13	31·2
Mar.	—	—	28	39·2	2	32·0	29	36·6
Apr.	—	—	18	32·7	17	29·4	9	34·9
May	—	—	23	25·5	31	26·1	17	24·0
June	—	—	13	22·1	30	25·5	6	19·5
July	—	—	20	20·9	30	23·6	30	31·5
Aug.	—	—	—	—	—	—	—	—
Sept.	—	—	15	33·9	22	30·3	—	—
Oct.	—	—	6	33·3	17	36·4	—	—
Nov.	—	—	21	36·2	13	21·6	—	—
Dec.	27	39·3	19	39·6	31	39·1	—	—

Table 5. *Daily lists: species per day per season*

Season	Days	Average	Best month and average
Wet, 1935–6	124	37·8	Dec. 39·3; Mar. 39·2
Dry, 1936	77	26·0	Sept. 33·9
Wet, 1936–7	88	36·3	Jan. 41·6
Dry, 1937	130	27·4	Oct. 36·4
Wet, 1937–8	124	36·4	Dec. 37·1
Dry, 1938	53	27·6	July 31·5
Totals	596	32·5	

May to October inclusive as the dry season. Table 6 shows the results for the more prominent species. I have also included, as Table 7, monthly figures for January in each of the three years, in order that they may be available for comparison with previous results, although those for 1937, being based on only 78 counts, are not reliable.

Table 6. *Sample counts: seasonal percentages*

Species	Wet, 1935–6	Dry, 1936	Wet, 1936–7	Dry, 1937	Wet, 1937–8	Dry, 1938	Totals
Pycnonotus tricolor	87	85	89	83	85	72	84
Streptopelia capicola	33	37	20	27	18	34	28
Uraeginthus angolensis	25	22	23	24	20	29	24
Motacilla aguimp	39	43	47	41	48	44	44
Passer griseus	20	6	22	12	32	10	19
Chalcomitra senegalensis	14	32	21	39	18	42	26
Laniarius ferrugineus	18	8	13	7	14	3	12
Zosterops senegalensis	20	4	8	2	21	4	12

Table 7. *Sample counts: monthly comparisons for January*

Species	1933	1934	1935	1936	1937	1938
Pycnonotus tricolor	75	86	85	86	87	82
Streptopelia capicola	55	58	43	45	32	18
Uraeginthus angolensis	38	27	30	24	31	17
Passer griseus	36	32	27	13	29	35
Dicrurus adsimilis	26	14	18	11	13	15
Motacilla aguimp	11	25	22	42	45	52
Laniarius ferrugineus	(9)	23	20	19	12	16

In order to test the reliability of this method, I started in January 1936 following up each count immediately by a second one and continued this until October 1937, thus including two dry and one and a half wet seasons. The summarized seasonal figures for the eight most prominent species are included in Table 8.

Table 8. *Sample counts check: percentages*

	Wet, 1935–6		Dry, 1936		Wet, 1936–7		Dry, 1937	
Species	1st count	2nd count	1st count	2nd count	1st count	2nd count	1st count	2nd count
Pycnonotus tricolor	85	86	85	83	89	87	85	83
Streptopelia capicola	38	39	37	31	20	26	27	27
Uraeginthus angolensis	22	18	22	20	23	20	24	20
Motacilla aguimp	38	42	43	43	47	51	41	43
Passer griseus	23	25	6	4	22	22	12	10
Chalcomitra senegalensis	14	13	32	25	21	23	39	35
Laniarius ferrugineus	17	13	8	10	13	8	7	10
Zosterops senegalensis	20	22	4	0	8	8	2	2
Number of counts	369*	336*	229	229	285	285	372	372

* Omitting December, for which there is no second set of figures.

The method is admittedly not a very satisfactory one. The maximum discrepancy per season is 7 % on 229 counts, 5 % on 285 counts and 4 % when there are more than 300 counts. This suggests that the latter is the minimum for reasonably reliable data.

4. Fluctuations of individual species

As already stated, one of the most useful functions of the present method of investigation is the light it throws on the fluctuations of individual species. I propose to consider now some of the more interesting of these.

The yellow-vented bulbul (*Pycnonotus tricolor layardi*) is the most abundant species in the township. It occurs in about 84 % of the sample counts, but was slightly less numerous during 1932–3 than it was later, and showed a sudden decline during the 1938 dry season. I thought at first that this might be due to the fact that only cold weather months are included, but on working out the corresponding figures for May, June and July, 1936 and 1937, I found that these agreed to within 1 % with the figures for the whole dry seasons. Evidently, therefore, there has been a falling off in the bulbul population. The African pied wagtail (*Motacilla aguimp vidua*) is the second bird on the list in sample counts. Since the dry season of 1934, its seasonal percentage has only once fallen below 40 %; and the figure for 1935–8 is 44 %, just over half that of the bulbul. The Cape turtle dove (*Streptopelia capicola tropica*) shows consistent seasonal fluctuations, being more abundant during the dry season than in the rains and, as suggested by the 1938 figure and confirmed for other years, especially in the cold weather. Since the dry season of 1933, this species has fallen off in numbers, with a minor recovery in 1936.

The Nyasa cordon-bleu (*Uraeginthus angolensis niassensis*) seems to have shown no appreciable variation of status during the last five years, though the last figure of all suggests a recent increase. The scarlet-chested sunbird (*Chalcomitra senegalensis gutturalis*) exhibits decided seasonal fluctuations, which, curiously, were not shown by the previous figures. In the sample counts, it is actually slightly more numerously represented than the cordon-bleu, but was not seen on so many different days. This is what one would expect of a bird with seasonal fluctuations. The grey-headed sparrow (*Passer griseus ugandae*) also shows seasonal fluctuations, but exactly the reverse of those shown by the sunbird. Indications of a drop in numbers were shown by the figures for the 1934 5 rains and this is confirmed in the present set.

The Mozambique boubou (*Laniarius ferrugineus mossambicus*) is also more conspicuous during the rains, and the figures suggest a slow decline in its numbers, which, however, may be illusory. The drongo (*Dicrurus a. adsimilis*) shows no marked fluctuations over the whole period. The black-collared barbet (*Lybius t. torquatus*) shows a decline during the dry seasons of 1936 and 1938. Heuglin's robin-chat (*Cossypha heuglini subrufescens*) was most conspicuous during the period between the rains of 1933–4 and the dry season of 1937

when a decline was noted, not, however, reducing its numbers to the small percentages of the preceding period. The puff-back shrike (*Dryoscopus cubla hamatus*) was somewhat less abundant than during the preceding tour and showed a tendency to decline further.

The golden-rumped tinker-bird (*Pogoniulus chrysoconus extoni*) confirms the slight seasonal fluctuations already suspected. It also seems to be on the decrease. The Kurrichane thrush (*Turdus libonyanus virescens*) has maintained the high figures recorded for the last two seasons of the previous tour. The rufous-eyed flycatcher (*Batis m. molitor*), more conspicuous during the rains, shows a regression from the high figures of the wet seasons 1934–5 and 1935–6. The black-headed oriole (*Oriolus oriolus larvatus*) has decidedly decreased, especially during the 1937–8 rains, the last figure, however, suggesting a recovery of numbers. The silvery wren-warbler (*Prinia subflava gracilis*) shows a marked seasonal fluctuation, but I believe this to be illusory. The rains are when it breeds and it is much more noisy and conspicuous at this season.

The grey-backed camaroptera (*Camaroptera c. griseoviridis*) has notably increased. Recorded on only 129 days (18%) during the previous tour, this has risen to 402 (74%) during the present period. The white-eye (*Zosterops senegalensis pallidus*) has also greatly increased, though showing a relapse during the dry season of 1937. The Mozambique serin (*Serinus m. mozambicus*) has maintained its position with irregular fluctuations. The black-headed bush-shrike (*Tchagra senegala emini*) is another species that has decreased in numbers, the onset being marked by the dry season of 1936. The red paradise-flycatcher (*Terpsiphone perspicillata plumbeiceps*) is, as noted in my previous paper, a species whose migrations fit very awkwardly into the framework of any tour that may be made. It arrives during the third week in September and departs during the third week in March. Over this period, its percentage occurrence in the daily lists is as high as 99.

I have been able to collect some data on the wood doves (*Turtur afer hilgerti* and *T. a. chalcospilos*), which are more numerous during the rains than in the dry season, this was masked by other fluctuations in 1932–5). Of the 441 records of these forms, 125 are attributable to *chalcospilos* and 316 to *afer*. They have declined in numbers since the previous tour. Other species to show marked declines in number are: the pied crow (*Corvus albus*), the European bee-eater (*Merops apiaster*), the arrow-marked babbler (*Turdoides jardinei*) and the South African hoopoe (*Upupa africana*).

On the other hand, certain species have noticeably increased. These include the cardinal woodpecker (*Dendropicus fuscescens hartlaubi*), the grey-headed sparrow (*Passer griseus swainsoni*), the rock sparrow (*Petronia superciliaris*), the yellow-throated longclaw (*Macronyx c. croceus*) and the rufous-bellied warbler (*Sylvietta rufescens pallidus*).

The discovery that the rare rat-eating buzzard (*Machaerhamphus alcinus anderssoni*) is a wet weather visitor is also most interesting.

5. Summary

In spite of differences in the morphometrics and feeding mechanisms of various species, it is maintained that the techniques of sample counting and part time or spare effort regular enumeration of the organic assemblages of individual species in different places and at different times. Their practical [illegible] results in new fish and [illegible]. The [illegible] [illegible] [illegible]

AN INVESTIGATION OF THE MOVEMENTS OF FRESH-WATER INVERTEBRATE FAUNAS

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1. Introduction

In a previous paper (Moon, 1935*b*) it was shown that in times of flood the invertebrate littoral fauna of Windermere moves on to parts of the shore recently covered by the rise in level of the lake. These flood movements are only a special case of the movements which are always taking place in the littoral region of lakes, and on the beds of streams. It is with these movements that the present paper is concerned.

2. Apparatus and methods

The movements were investigated by the use of trays covered with samples of the substratum from which the fauna had been removed (Moon, 1935*a*). The trays consisted of square iron frames laced across with wire netting and covered underneath with stramin or some other suitable material. The trays were covered with stones, sand or even weed in special cases, and left on the bottom of the lake or river for the desired length of time. By lifting the trays at various time intervals, and then counting the fauna which had moved on to them, an index of the amount of movement of the fauna was obtained.

In using these trays, precautions were taken against undue disturbance of the substratum, and the trays were left for at least 24 hr., free from stones, in the place they would occupy during the experiment. When the experiments were started the trays were lifted gently, washed free from any fauna which might have moved on to the bare stramin and netting, and then replaced in their position on the substratum covered with stones.

In the case of experiments on the diurnal variations of the fauna, the trays were lifted and the fauna removed at sunset and dawn, preferably at the equinoxes so that the hours of darkness equalled the hours of daylight. When it was impossible to carry out the experiment at the equinoxes, the trays were exposed during the day for a period of time equivalent to the hours of darkness. In the summer it was necessary to vary the periods of daytime exposure so that morning and afternoon periods were covered alternately. By this means was investigated the possibility that movement might be more active during the afternoon than in the morning. The same set of stones for each tray was used throughout the experiment.

3. Results

The first series of experiments was made in the stony littoral region of Windermere, using trays 1 sq. ft. in area. Table 1 gives the results of some of these experiments; it will be seen that considerable movement was taking place. In one case, for example, seven individuals representing five different species had colonized the trays in 12 hr. In another example fourteen individuals representing eight species moved on to the trays in 24 hr. If the trays are left on the bed of the lake for longer periods of time a fauna colonizes the trays approximately similar in number and composition to the undisturbed

Table 1. *Epley Head. Area of trays* 1 *sq. ft.*

Date (1932)	13 Sept.	13 Sept.	9 Sept.	9 Sept.
Time in lake (hr.)	12	12	24	24
Depth (ft.)	1	2	1	2
Ephemeroptera				
Ecdyonurus sp.	4	2	4	7
Centroptilum sp.	1	—	4	1
Caenis horaria (L.)	—	—	1	1
Plecoptera				
Nemura sp.	—	—	—	1
Trichoptera				
Limnophilus sp.	—	—	1	—
Agapetus sp.	—	1	—	1
Sericostoma personatum (McLachl.)	—	—	—	—
Stenophylax sp.	—	—	—	—
Lepidostoma hirtum (Fab.)	—	—	1	—
Mystacides nigra (L.)	—	—	—	—
Leptocerus aterrimus Steph.	—	—	—	6
Setodes sp.	—	2	—	—
Hemiptera				
Micronecta sp.	—	—	—	—
Diptera				
Chironomidae	1	1	—	—
Hydracarina				
Hygrobates sp.	—	—	—	1
Mollusca				
Limnaea pereger (Müll.)	—	—	1	—
Crustacea				
Gammarus pulex L.	1	—	1	1
Annelida				
Herpobdella atomaria Carena	—	1	—	—
Platyhelminthes				
Polycelis nigra Ehrenb.	—	—	—	—
Planaria lugubris O. Schm.	—	—	1	—
Total no. of individuals	7	7	14	19
No. of different species	4	5	8	8

areas around the trays. In Table 2 the difference between the 12 weeks and 4 weeks tray is due to the absence of *Agapetus* sp. on the former. Fluctuations such as this are fairly common in the littoral region during the autumn and early winter.

In Table 3 a number of other results have been summarized to show the amount of movement which takes place. Part of Table 3 is based on observations made from trays which were put down each month as far as possible, over a ten-month period. These trays showed that at all seasons of the year,

Table 2. *Epley Head. Area of tray 4 sq. ft.*

Time in lake (weeks)	4	12
Date	29 Nov. 1933	12 Nov. 1934
Depth (ft.)	1	—
EPHEMEROPTERA		
Ecdyonurus sp.	37	32
Centroptilum sp.	10	12
Leptophlebia sp.	6	19
Caenis horaria (L.)	—	23
PLECOPTERA		
Chloroperla sp.	22	—
Isoperla sp.	—	2
Nemura	5	2
TRICHOPTERA		
Leptocerus aterrimus Steph.	7	11
Oecetis sp.? furva (Ramb.)	—	1
Stenophylax sp.*	21	16
Sericostoma personatum (McLachl.)	1	—
Silo sp.	1	7
Agapetus sp.	58	—
Polycentropus flavomaculatus (Pict.)	1	—
COLEOPTERA		
Elmis (larvae and adult)	3	—
Gyrinus larva	1	2
DIPTERA		
Chironomidae	1	3
Ceratopogon sp.	1	—
MOLLUSCA		
Ancylastrum sp.	1	—
Pisidium sp.	6	—
Valvata piscinalis (Müll.)	3	—
HYDRACARINA		
Diplodontus despiciens (Müll.)	—	3
spp. indet.	—	4
CRUSTACEA		
Gammarus pulex L.	11	10
Total no. of individuals	196	147
No. of different species	19	15

* Larva resembles the continental *S. nigricornis* (Pictet).

Table 3. *Average of results from trays* on the Epley Head and Watbarrow Woods shoreline. Depths between 6 in. and 4 ft.*

Date	Time in lake hr.	No. of trays	Average no. of different species	Average of total no. of animals
14 Sept. 1932	6 hours	3	2	2
13 Sept. 1932	12 ,,	4	3	4
14 Sept. 1932	15 ,,	3	5	9
8–10 Sept. 1932	24 ,,	7	7	25
11 Sept. 1932	48 ,,	3	9	28
2 Nov. 1933	14 days	6	7	120
29 Nov. 1933	27 ,,	6	9	100
2 Jan. 1934	36 ,,	6	10	77
12 Feb. 1934	40 ,,	5	8	40
19 Mar. 1934	35 ,,	6	8	47
1 May 1934	42 ,,	6	8	78
18 June 1934	49 ,,	3	13	80
2 Aug. 1934	43 ,,	4	6	114

* 1932 trays = 1 sq.ft.; 1933–34 trays = 4 sq.ft.

down to a depth of 5 ft., there was movement. Below 5 ft. the stony littoral is usually replaced by *Litorella*, but, as was shown in a previous paper (Moon, 1935*a*), movements also take place on the *Litorella*.

The comparison between the large and small trays in Table 3 is difficult. The small trays were used at the beginning of this work, and were put down in places selected for the richness of their fauna. The larger trays on the other hand were put down at two places where below 2 ft. there is a transition between the littoral and sublittoral, with a consequent reduction in fauna. Also there was a two-year interval between the experiments with large and small trays, and conditions may well have altered in this period.

Experiments similar to those described for lakes were made in the River Avon (Hampshire), and its tributaries. One set of experiments was carried out in Latchmore Brook, an acid New Forest tributary of the River Avon; the other in an irrigation channel leading water from the main river to a water meadow. The results are given in Table 4, and it is clear that fairly rapid currents of water do not prevent the fauna moving about and colonizing bare areas just as is the case in lakes. The much greater number of animals on the trays in the irrigation channel is due to two facts. First, the irrigation channel is to all intents a chalk stream, and therefore richer in animal life than the acid waters of Latchmore Brook. Secondly, the experiment was done at a time when *Limnaea pereger* (Müll.) and *Baetis* sp. were at a maximum, the former occurring extremely abundantly. In Latchmore the characteristic colonists were nymphs of *Nemura* sp., *Chloroperla* sp., *Leptophlebia* sp. and the amphipod *Gammarus pulex* L.

Table 4. *Results from trays in Latchmore Brook and an irrigation channel of the River Avon. Depth* 8 *in. Area of trays* 4 *sq. ft.*

Date (1938)	Depth	Time in stream days	Surface rate of flow (approx.) (ft. per sec.)	No. of trays	No. of different species	No. of individuals
			Latchmore			
8 Feb.		2	—	1	6	26
10 Feb.		4	—	1	4	6
12 Feb.		6	—	1	9	22
14 Feb.		8	—	1	8	22
25 Feb.		2	1·5	1	9	14
27 Feb.		4	1·0	1	8	84
1 Mar.		6	1·2	1	11	55
3 Mar.		8	1·5	1	11	117
			Irrigation channel			
Date (1938)	Depth					
27 July	2 in.	1	3·0	1	10	443
29 July	2 in.	2	0·3	1	11	1147
30 July	1 ft.	4	Negligible	1	12	1449

4. Indications of diurnal variations in the movements

By using trays it has been possible to show that although movement does take place during the daytime, the greatest activity for most of the aquatic

invertebrates so far examined, is at night. Experiments were made in Windermere, and in the River Avon. The results of these experiments are given in Table 5, and the greater activity at night is apparent. Naturally the collections were dominated by the more abundant and active members of the fauna, and in these cases it was clear that they moved more at night than in the day. In the case of the less numerous and active forms, the numbers were too low for any statement to be made, beyond the fact that they showed a tendency to move more at night. In Windermere four insect nymphs, *Ecdyonurus* sp., *Centroptilum*, *Leptophlebia* sp. and *Chloroperla* sp., and a mite *Diplodontus despiciens* (Müll.) were more active at night. *Micronecta poweri* (D. & S.) however moved more during the day, while a mite *Hygrobates naicus* Johnst. moved equally in the night and in the day (Table 6). *H. naicus* however was peculiar in that it moved more during the afternoon than in the morning.

Table 5. *Diurnal variations in the movements of the fauna. Area of trays, 4 sq. ft.*

	Windermere		River Avon	
	Species	Total population	Species	Total population
D	17	140	—	—
N	*14*	*83*	*10*	*81*
D	13	53	9	45
N	*14*	*167*	*11*	*77*
D	11	139	9	25
N	*16*	*229*	*13*	*58*
D	11	108		
N	*10*	*148*		
D	10	60		
N	*16*	*254*		
D	10	52		
N	*12*	*230*		
D	12	73		
N	*15*	*260*		
No. of trays	9		4	
Depth (in.)	6		6	
Date	5–11 May 1935		6–9 Oct. 1938	
Exposure (hr.)	8		12	

D = day. N = night.

Table 6. *Variations in the movements of a mite* Hygrobates naicus *Johnst. from Windermere. Details as in Table* 5

Experiment no.	Night	Day	Morning	Afternoon
1	—	45	—	45
2	20	7	7	—
3	17	31	—	31
4	27	7	7	—
5	20	26	—	26
6	29	3	3	—
7	25	22	—	22
8	9	—	—	—

In the River Avon *Baetis* sp., *Asellus* sp. and *G. pulex* colonized the trays more at night than in the day, but *Sigara* sp., on the other hand, was more

active in the day. This makes an interesting comparison with the results for the other Hemipteran *Micronecta poweri* (D. & S.), which also moved more in the day in the Windermere experiment. Tables 6 and 7 give the day and night movements of typical representatives from the two localities mentioned in Table 5. The experiments in the River Avon are of interest in that they yielded results under very unfavourable conditions. The only place at which they could be carried out had a limited population, the insect fauna still being depleted by the summer emergence of adult insects. Also the surface current at the places where the trays were set averaged rather more than a foot per second.

Table 7. *Diurnal variations in the movements of* Ecdyonurus *sp.* (*from Windermere*) *and* Baëtis *sp.* (*from the River Avon, Hampshire*). *Details of experiment as in Table* 5

Experiment no.	*Ecdyonurus* sp.		*Baëtis* sp.	
	Night	Day	Night	Day
1	—	13	27	4
2	38	7	25	4
3	90	26	14	—
4	199	21		
5	80	21		
6	153	31		
7	121	10		
8	163	—		

In the case of those insect nymphs which show greater activity at night, it might be supposed that there was some relation between their stage of development, and their greater activity at night. The fact, however, that those forms showing greater activity at night were represented by mature and immature individuals, shows that the greater nocturnal activity is not directly connected with the stage of development.

5. Discussion

From these experiments two things are clear. First, the fauna moves about freely over the substratum and colonizes bare areas. Secondly, with one or two exceptions, the animals so far investigated tend to move more actively at night.

Movements of the bottom fauna have been observed by other workers. Wesenberg-Lund (1908) records movements of the bottom fauna on the shores of Baltic lakes in relation to change of water level in spring as a result of the melting snow. The same author (1912) describes the migration of the fauna to the warm southern shores of Baltic lakes in the spring. The shores with a southerly aspect become free from ice sooner than those facing north. Wodsedalek (1912) states that in American lakes the nymphs of *Heptagenia interpunctata* (Say) migrate away from the shore when the temperature falls in the autumn. Pauly (1917) working on the Müggelsee found that the fauna

moved shorewards in the spring and out into deeper water in the winter. Pauly does not consider oxygen and temperature as important, in disagreement with Wesenberg-Lund who considers these two factors important. Lundbeck (1926) during his survey of the North German lakes found that many Chironomids, Tanytarsidae, Tanypodinae and the Mollusca, *Dreissensia* and *Valvata*, moved deeper in the winter and into shallower water in the summer. The factors responsible appear to be quite obscure, emergence movements, temperature and oxygen all being suggested as possibilities. Eggleton (1931) found a similar shoreward movement of the fauna in the summer and a retreat to deeper water in the winter. He correlated these movements with oxygen, and assumed that the shoreward movement of the fauna in summer was to avoid the stagnation in the deeper water.

The movements observed by these authors are different from those described in this paper, which seem to be purely random movements. The observations just referred to are evidently concerned with annually recurring movements associated with a definite set of factors. In the localities where the tray experiments were carried out there is no evidence for any annual regularity in the movements, probably because in Windermere there is never any oxygen shortage, nor does this lake freeze. The same applies to the River Avon and its tributaries.

The problem is complicated in the case of insect nymphs by an increase in activity as the nymph matures (Moon, 1935 *b*). It is suggested tentatively that the movements represent the wandering of the fauna in search of food. This agrees with the observations of Neave (1930) who found extensive migrations of the nymph of *Blasturus cupidus* Say. The nymphs migrated into temporary streams formed during the spring thaw in Manitoba. He correlated their movements with an abundant algal growth that appeared in these streams. Obviously these movements will be affected by external factors, e.g. change of water level in times of flood. The problem is greatly complicated by the fact that very little is known about taxes of the invertebrate fauna. Obviously, as with plankton movements, the reactions of the organism to light, temperature and food, and its physiological state, will influence its movements. The strong negative phototaxes of most freshwater invertebrates are well known. Wodsedalek (1912) records the negative phototaxis of *Heptagenia interpunctata* (Say). Gros (1923) noticed that after the fifth ecdysis the nymphs of *Ecdyonurus forcipula* (Pict.) avoided the light when not feeding, but while feeding they were very active. Gros also recorded that ecdysis usually took place at night.

One factor which might be assumed to influence the movements of the fauna is temperature. Although low temperature may limit the amount of movement, there is no evidence that low temperatures completely inhibit the activity of the fauna. For example in Table 4 the earlier set of trays at Latchmore were exposed to an average temperature of 6° C., while the large

trays in Windermere were exposed in winter to an average temperature of 5° C. Yet in both these cases numerous animals colonized the trays.

6. Summary

1. A method is described for investigating the movements of the invertebrate fauna over the substratum.

2. Results from Windermere, and River Avon (Hampshire), show that artificially depopulated areas are re-colonized in a short space of time.

3. In the lakes and streams investigated there is much more movement at night than in the day, although a few insects, e.g. *Sigara* sp. and *Micronecta* sp. show the reverse. The mite *Hygrobates naicus* (Johnst.) showed equal activity in the day and night, but moved more in the afternoon than in the morning.

4. These movements are random movements, and distinct from the annually recurring movements described in certain European and American lakes. It is suggested that the movements are correlated with feeding activities.

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RECOLONIZATION BY BIRD SPECIES ON BURNT WOODLAND

By AVERIL MORLEY

1. Introduction

On 6 May 1935, about 200 acres of Dallington Forest, East Sussex, were destroyed by fire. I was not present in the forest until the fall of that year, and left in the fall of 1936, but notes made during this period and during ten days at the end of May and beginning of June 1939, on the breeding-season succession of bird life in burnt woodland, may be of interest as this subject does not seem to have been studied in Britain. Outside the breeding season, various species appeared on the burnt area which bred elsewhere, but no proper notes were made on this point, and fall–winter distribution needs a resident observer even more than breeding distribution.

The soil of the forest is Ashdown Sand: sand, friable porous clay, sandstone rock subsoil, ironstone in the valley; a top spit of peat in some places, loam in lower parts; entirely acid.

2. Unburnt forest

General. Approximately 500 acres. Height 100-500 ft. Very anciently, up to about 100 years ago, timber was used for iron-smelting and old charcoal-burners' pits remain in some parts. Before 1936, brushwood was regularly collected for the owner's brick furnace; the shooting was let, but not preserved. About 20 years ago plantations (sweet chestnut) had been made, but there is no recent planting. Some bracken is cut for farm purposes. In 1936, most of the forest changed hands and became preserved for pheasants, but as the new owner has become more enthusiastic about living birds than on shooting, *officially* control of predators is not too rigorous, except for grey squirrels and foxes, the latter because of the clamour of chicken farmers. Paths in the forest are kept clear. Apart from that caused by the above activities, disturbance by man is very small indeed. Pole-traps have lately been abandoned.

Main habitats

Scots pine communities: (1) Pine (*Pinus sylvestris*). No undergrowth.

(2) Pine; undergrowth ling (*Calluna vulgaris*), heaths (*Erica*), *Molinia*, and whortleberry (*Vaccinium myrtillus*), or bracken (*Pteridium aquilinum*) or both.

Broad-leaved communities: (3) Beech (*Fagus sylvaticus*). No undergrowth.

(4) Natural oak (*Quercus robur* and *Q. sessiliflora*). Undergrowth bracken (*Pteridium*), bramble (*Rubus*).

(5) Cropped oak, various stages, mixed with hazel (*Corylus avellana*), in some parts hornbeam (*Carpinus betulus*), birch (*Betula alba* and *B. pubescens*). Undergrowth bracken (*Pteridium*).

(6) Sweet chestnut (*Castanea sativa*) close plantations periodically cropped, but apparently not much recently.

(7) Sparse small aspen (*Populus tremula*). *Molinia* dominant. Two *Carex* species occur.

(8) Thick birch (*Betula*), no undergrowth.

(9) Birch (*Betula*), undergrowth ling or heath or both.

Mixed broad-leaved and pine communities: (10) Thick mixed wood, undergrowth bracken.

(11) Sparse mixed wood, undergrowth gorse (*Ulex europeus*), broom (*Sarothamnus scoparius*), bracken (*Pteridium*), ling.

Treeless community: (12) Open ling, mixed with gorse (*Ulex*), broom (*Sarothamnus*), whortleberry (*Vaccinium*).

Species present in the breeding seasons 1936 *and* 1939

Carrion crow (*Corvus corone*)
Jay (*Garrulus glandarius*)
Chaffinch (*Fringilla coelebs*)
Yellowhammer (*Emberiza citrinella*)
Tree pipit (*Anthus trivialis*)
Tree-creeper (*Certhia familiaris*)
Great-tit (*Parus major*)
Blue-tit (*Parus coeruleus*)
Coal-tit (*Parus ater*)
Marsh-tit (*Parus palustris*)
Willow-tit (*Parus atricapillus*)
Long-tailed tit (*Aegithalos caudatus*)
Golden-crested wren (*Regulus regulus*)
Chiffchaff (*Phylloscopus collybita*)
Willow-wren (*Phylloscopus trochilus*)
Wood-wren (*Phylloscopus sibilatrix*)
Garden warbler (*Sylvia borin*)
Whitethroat (*Sylvia communis*)
Mistle-thrush (*Turdus viscivorus*)
Song-thrush (*Turdus ericetorum*)
Blackbird (*Turdus merula*)
Robin (*Erithacus rubecula*)
Wren (*Troglodytes troglodytes*)
Nightjar (*Caprimulges europeus*)
Green woodpecker (*Picus viridus*)
Great-spotted woodpecker (*Dryobates major*)
Lesser-spotted woodpecker (*Dryobates minor*)
Cuckoo (*Cuculus canorus*)
Tawny owl (*Strix aluco*)
Sparrow hawk (*Accipiter nisus*)
*Mallard (*Anas platyrhynchus*)
Wood-pigeon (*Columba palumbus*)
Stock-dove (*Columba oenas*)
Turtle-dove (*Streptopelia turtur*)
Woodcock (*Scolopax rusticus*)
Pheasant (*Phasianus colchicus*)

* Seen in 1935 only. Female only for nesting.

The birds of the forest edge are omitted from the above list, as here there were species present in it which did not occupy the forest proper, and whose special edge niches were not destroyed by the fire.

3. Burnt Forest in 1936

Judging from the remains the fire destroyed examples of all the above habitats except 3, 8 and 12. The demarcation of burnt from unburnt forest was well defined by a stream, two parallel sandy paths, and ditches dug to prevent the flames from spreading. Between the paths jutted a "peninsula"

of untouched beech, Spanish chestnut and a few Scots pine. The clear-cut separation of burnt from unburnt was followed by the birds generally.

Habitats	Species present in the breeding season
(1) Bare charred trees. Undergrowth, unbroken acres of bracken (*Pteridium*), some dead *Calluna* woody stems	Nightjar
(2) Dead Scots pine (*Pinus sylvestris*), many retaining bunches of dead brown needles. No undergrowth	Mistle-thrush, 1 pair (nest being composed of usual dead grass, etc. obviously bird ranged outside this habitat)
(3) One island of canopy, single beech (*Fagus sylvaticus*) partially destroyed, *c.* 40 yd. from edge of burnt area	
(4) Mixed burnt and live *Molinia* on lower parts, with dead heaths on slopes	
(5) Narrow fringe area of mixed live (very few) and dead birches (*Betula*), dead pines (*Pinus*). Undergrowth bracken (*Pteridium*), dead and live (small) ling or heath or both	

4. Burnt Forest in 1939

(1) Dead pines, no regeneration. Bunches of needles lost. No undergrowth	
(2) *Molinia* mixed with dead and new ling or heath or both on slopes, latter scarcely 6 in. high	
(3) "Island" beech (with house)	Wood-pigeon visiting

In 1935–6 the beech obtained artificial "undergrowth" when we built beneath a four-roomed, substantial "house" of tree trunks interlaced with branches, the interstices stuffed with dead heather and bracken till light-proof. This cover had some slight effect outside the breeding season, but none during it.

(4) Mixed dead wood and revived "cropped" oak, and birch, latter many new plants of rapid growth. Undergrowth bracken, below which in some places two-year-old whortleberry, heath and ling hardly over 6 in. high. Mass of dead woody *Calluna* stems	Tree pipit, willow-wren, robin
(5) Fringe area of mixed dead wood and living birch, much new growth. Undergrowth dead and live heather, bracken	Chaffinch, whitethroat. Combining this habitat with unburnt forest

The disappearance of the mistle-thrush is evidently linked with the falling off of the dead bunches of needles on the dead pines, for height of song-post and nest-place were unaltered. Except the beech, none of the "clothed" growth in the other habitats was of the necessary height. The absence of the nightjar has no apparent cause as there seemed still enough open space for the species. However, since at least 1935, the bird has been decreasing in the forest as a whole, which may account for its disappearance from the burnt area.

The three chief colonizing species of 1939 must have breeding season needs that either demand, or do not clash with, the composition of the burnt area habitats.

Tree pipit. Needs: High trees for song and song-flight (though from perch of 18 in. full song can be performed). Ground cover for nest. Adjacent undergrowth no deterrent, if spaced.

Willow-wren. Needs: Song-post 6–8 ft. high (Southern & Venables, 1939). Ground cover for nest. The type of much of the ground cover, two-year-old whortleberry and heather, does not seem typical for the species, so it is interesting to note that above authors found it nesting in 3 in. *Vaccinium* in Lapland. Not averse to adjacent bracken.

Robin. Needs: Song-post. Ground cover for nest (crannies, Lack & Venables, 1939). Some form of shade, here provided by undergrowth of bracken as well as the cropped oak and birch.

Fringe and unburnt forest species

Chaffinch. Needs: Song-post. Canopy of secondary growth for nest. Presumably absence of canopy and of certain denseness of secondary growth or of both was inhibiting factor for female. Song was performed by male on fringe area as well as on adjoining unburnt forest.

Whitethroat. Needs: Air and secondary for song and song-flight. Secondary and undergrowth for nest. Birch and cropped oak unadaptable for nest-place and undergrowth on burnt area too low, or if bracken, unadaptable. Absence of bushy secondary growth and undergrowth of certain height and denseness evidently limiting factor for female. Song performed by male on fringe area in conjunction with unburnt forest.

Wood-pigeon. Needs: High perch for song and launch of territorial flight. Canopy or secondary for nesting. Small size of the island beech would inhibit actual nesting. Probably other species visited the beech but this species the only one actually seen there, and feathers found below. Probably an extension of territory from unburnt forest *c.* 40 yd. distant, and therefore this habitat would rank as fringe canopy.

No account has been taken of the food needs of colonizers as no attempt was made to calculate food supply on the burnt area. It is obvious, however, that the food of the colonizers is the food of other species absent from the area and therefore that conditions of food supply cannot be the sole cause of that absence, while it is unlikely that the wood-pigeon could procure, in summer, food from the burnt area at all, so that its presence is not to be explained on that score.

The absence of the bushy type of undergrowth such as results after broad-leaved trees are cropped would account for the non-appearance of several species, e.g. yellowhammer (present on neighbouring recently cropped oak), while the presence of large tracts of undiluted bracken closed the area to species needing open ground. For the wren, a species able to live in pure bracken, the growth was not thick enough. Starting from naked earth in 1935, the bracken had not yet formed the thick mat and piles of dead fronds through

which the wren can creep hidden. Outside the breeding season, however, a pair visited the "house", but careful search in the May–June 1939 period failed to reveal the species though present in adjacent unburnt wood.

I would like to thank very much Mrs Ruth Tristram, F.L.S., for her help, especially with the botanical part, and Charles Elton for much encouragement and for suggestions.

5. Summary

The bird life on 200 acres of burnt woodland in East Sussex was noted in the first and fourth summer after burning. In the first breeding season in five habitats, two species, mistle-thrush and nightjar, were present. In the fourth, in five habitats, six species were present: tree pipit, willow-wren, and robin over the whole area; chaffinch, whitethroat and wood-pigeon on the fringe only. On unburnt forest, in twelve main habitats, thirty-six species were noted.

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THE FACTORS CONDITIONING THE RISING OF TROUT (*SALMO TRUTTA*) IN A SMALL FRESH-WATER LAKE

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(*With Plate* 1 *and* 5 *Figures in the Text*)

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1. Introduction

The "problem of the rise" has long occupied the attention of observant anglers. It is obvious that a proper understanding of the factors controlling the characteristic behaviour of trout, which at one minute may be quite quiescent and the next minute be rising eagerly at flies which have been on the surface for some time, would be of considerable practical value.

It is the sudden changes of behaviour which take place with no obvious reference to external climatic conditions that have presented the problem. The greater part of the food of trout (*Salmo trutta* L.) is obtained below the surface of the water, in the form of insect larvae, crustaceans and snails, the nature of the food depending on the habitat of the trout and the season of the year (Pentelow, 1932; Slack, 1934). Surface food, mainly insect imagos, forms only a very small percentage of the total food consumed, being as Allan (1936) aptly puts it, more of a "savoury", the underwater food being the "roast beef".

Rising of trout therefore involves perhaps more than a change of diet; it may be a change of behaviour, the temporary forsaking of one habit for another. Behaviour in the lower vertebrates appears largely to be conditioned by external environmental factors, hence a study of the physical and chemical conditions prevailing before, after, and during the rise may give some idea of the state of environment most favourable for the exhibition of this type of behaviour.

The various factors which have been held responsible for the rising of trout have been summarized by Allan (1936). These have been suggested as

(*a*) hunger, causing the fish to take surface food, (*b*) abundance of flies on the water inducing the fish to rise, (*c*) certain temperature states, (*d*) certain oxygen tensions of the water, (*e*) variation in the electrical state and pressure of the atmosphere, and (*f*) various favourable conditions of wind, water and light.

That hunger is an important factor seems unlikely in view of the fact that the stomachs of rising fish may be already filled with underwater food, which is usually sufficiently plentiful at all times; there is, however, a possibility that hunger satiation, as we know it, is not experienced by fish.

Fundamentally, however, I regard rising as due to an inborn "drive" to seek food, part of the survival mechanism present in all animals from birth to death, which may or may not be expressed as actual hunger. This "drive" may be satisfied, psychologically and physiologically, by underwater food within relatively wide conditional limits, but cannot be satisfied by rising unless the environment is in a particularly favourable state, i.e. when the factors now to be considered are themselves favourable. It must be understood that the factors *condition*, but do not *cause* rising.

Abundance of flies is certainly favourable for a good rise, though whether it is a factor important for the inducement of the rise is doubtful—it is again a common observation that the water may be covered with flies, yet there is not a fish rising to them; that hatch of fly is, however, a limiting factor will be shown later. The remaining factors noted above all influence the rise in varying degrees.

The lake studied was very conveniently situated for daily observation and the trout under certain conditions showed a well-marked "evening rise". It should be understood that this study deals with the evening rise only, an occurrence which under suitable conditions could be quite regularly expected; it is, therefore, unlike the sporadic outbursts of rising which may occur at any suitable time on lochs and rivers. Since, however, the same temporary change of feeding habit is involved in both types, it is believed that the factors conditioning such an evening rise also play the major part in influencing the rising of trout during the day.

2. Ecological features of the lake

The lake on which these observations were made (Fig. 1) is a shallow artificial stretch of water situated a few miles from Guildford, in Surrey. It lies at an elevation of 200 ft. on terrain intermediate in type between the Greensand and Chalk, and was formed about 1780 by damming a small stream in order to provide power for a mill, the site of which is now lost.

The area of water is given in the O.S. map of 1916 as 2·998 acres, but now it is probably somewhat less, owing to ecological succession, silting and encroachment of the *Salix-Alnus* swamp on the north-east side. It is fed by

a small, rather sluggish stream, the two mile course of which is interrupted by four other small lakes and a bathing pool, and the level of the lake fluctuates occasionally, as a result of operation of these sluices higher up the stream. Two uncontrolled sluice outlets at the south and west corners of the lake join to form a small stream flowing west. Current in the lake is almost negligible.

The average depth of the lake is about 2 ft., the greatest depth being about 4 ft. at the southern outlet. Originally the lake must have been considerably deeper, but now the bottom is formed of a fluid black mud, in some places almost 3 ft. deep, the produce of many years, decay of weeds, dead leaves and

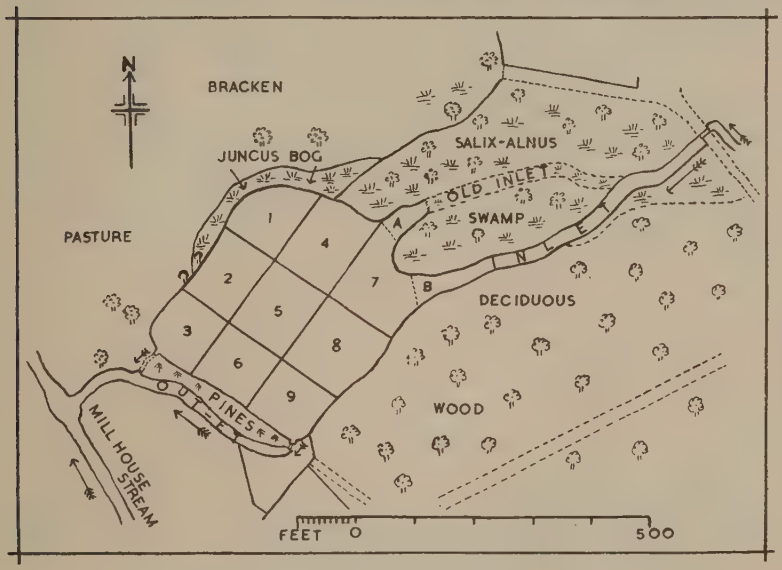

Fig. 1. General features of the lake.

constant silting up. The average depth of this muddy bottom is about 18 in., and the whole is heavily charged with decomposition gases, which are released spontaneously as bubble masses during hot weather. Along the southern shore there is a small bed of flinty gravel. At no time is the lake subjected to very high winds, being situated in a hollow and protected by trees on three sides. Owing to the low-lying nature of the surrounding ground, a warm day followed by a drop of several degrees in the evening results in an evening mist which may at times be very dense. The lake was arbitrarily divided into six squares for convenience in noting the position of fish, as in the map.

The lake is typically eutrophic, with its rich autochthonous bottom deposit, thick emergent vegetation and rather cloudy water, the *p*H generally

being about 7·0. *Carex paniculata* is the dominant emergent plant, while submerged vegetation in the main bulk of the water consists almost entirely of *Zannichellia palustris*, which grows thick in mid-June and almost chokes the whole lake. This has now been exterminated by chemical means (Avon Biological Research, 1936 7, p. 53; 1937–8, p. 52). Large masses of algal blanket weed (*Oedogonium* sp.) appear from May onwards, and float to the surface after a sunny day.

The fauna of the lake is rich in individuals and poor in species. Cladocera are the dominant planktonic forms, together with five species of Corixidae. The bottom fauna is composed almost entirely of Chironomid larvae, and large numbers of alder-fly (*Sialis* sp.) larvae in the shallow parts early in the year. The mussel, *Anodonta anatina* L., is fairly common, but no other molluscs occur. Small numbers of Ephemerid (mayfly) and Plecopteran (stone-fly) larvae are found along the southern shore.

The above features of the lake are all important, and are such that the water is subjected to considerable diurnal variations of temperature probably accompanied by diurnal and seasonal variations in dissolved gases, particularly oxygen, though no chemical analyses were made to determine these points. In spite of photosynthesis by the blanket weed, dissolved oxygen must fall very low in summer, due to increasing summer stagnation, respiration by animals and plants, decomposition of organic detritus, reduction due to rising bubbles of decomposition gases, high temperature and perhaps presence of iron (Welch, 1935). Probably the lake shows a diurnal oxygen pulse as in other similar small lakes, oxygen reduction being maximal during the night. All these reducing factors would operate most markedly in late spring and early summer, the time of this investigation, but their presence is argued by analogy only from other small lakes (Welch). No thermocline exists in summer.

3. The stock of fish and nature of the rise

The original stream must have contained only a few trout, as does the Mill House Stream to-day, but the lake was stocked in 1929 with 750 two-year-old brown trout of the so-called Loch Leven variety, and rainbow trout (*Salmo irideus* Gibbons). The rainbow trout, as in other places, have since entirely disappeared and owing to a variety of causes the brown trout have been considerably reduced; in 1937 the lake probably contained not more that 100 fish, though the stock was artificially increased with 200 yearlings in 1938. The trout appear to be the progeny of the original stock and average about 14 oz. in weight ($3\frac{1}{2}$–$4\frac{1}{2}$ years old).

Examination of faeces show that in the early part of the year the fish feed almost exclusively on *Sialis* larvae, while from the middle of May onwards the staple food is Corixidae, together with Cladocera from the plankton.

The lake also contains a few small roach (*Rutilus rutilus* (L.)) and gudgeon (*Gobio gobio* (L.)), probably inhabitants of the original stream.

Phot. 1. View of lake looking east to deciduous wood. *Juncus* bog in foreground, with emergent *Carex*, *Typha* and *Sparganium* fringing lake and two small *Alnus* bushes. On the left is the *Salix-Alnus* swamp, fringed with *Typha*, *Carex* and *Rumex*. Behind this is the entrance of the inlet stream. Water surface obstructed, beginning of July, but square 1 clear.

Phot. 2. View of lake looking south towards dam and the row of *Pinus* on the dam. South outlet on the left, overhung with bushes of *Rubus*. *Juncus* bog in foreground and fringing bushes of *Alnus*. Water surface overgrown with weed, beginning of July, but square 5 partly clear.

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Under favourable conditions the evening rise can be expected to start 20–30 min. after sundown. A few fish commence rising and in a few minutes the whole lake, except *A* and *B* (see map) is "ringed" with rising fish. The rise is at its height about 10–15 min. after starting, and ceases in about 30 min., with the exception of a few fish which rise sporadically until complete darkness falls. It is thus a twilight occurrence and starts almost coincidently with the emergence of the bats and retiring of the swallows to roost.

Under certain conditions the trout may rise sporadically during the day, but there is never the concerted action characteristic of the evening rise. The rising is steady surface feeding, the flies being sucked in with that curious "plop" so often described in angling books. Under favourable conditions the trout rarely if ever jump out of the water, this type of rise being in my opinion "abnormal". A boat rarely disturbs the rising fish. It may clearly be seen that rising fish cruise in small circles round a particular "beat", subsequent rises by the same fish being to the right or left of the original rise; this is of course to some extent dependent on the batch and distribution of the fly. The roach also rise in the evening, and their rise may be distinguished as a much gentler "dimpling" of the surface.

4. Method of observation

Observations were made daily from 22 April to 20 July 1937, with an unavoidable break from 9 to 20 June, and repeated from 25 April to 26 July 1938. The quality of the rise was estimated by counting the number of rises which could be seen generally during 5 min. at the height of the rise. These were classified as 0 (0 rises), sporadic (1–20 rises per 5 min.), poor (21–40 rises per 5 min.), moderate (41–80 rises per 5 min.) and good (81–over 100 rises per 5 min.). The rises are grouped into five qualitative classes owing to the practical difficulty of counting the rises all over the lake at any one time, or even in one part of the lake (since the distribution of rises is not uniform each night). They are therefore only an estimate of the type of rise, in most cases easy to determine, but the numbers cannot be treated statistically.

In the absence of exact recording instruments it was necessary to choose arbitrary standards for the weather conditions; consequently a personal factor is involved, but it is hoped the terms used are sufficiently clear for comparison.

Wind was classified according to direction and strength; this latter being either 0, variable, slight or good. Very strong winds were not observed. *Sky* was noted as clear, few clouds, cloudy, overcast or heavily overcast. *Surface ripple* was noted as 0, slight, medium or heavy, and the presence of an evening mist on the water surface noted. *General weather* during the day was roughly noted as cold, mild, warm and either dull, occasional sun or sunny.

Rain during the day or at the time of the rise was noted as 0, slight, medium or heavy and approximate duration. *Height of water* was recorded on a scale at the south-west pier. The *state of water* was either clear, cloudy or

turbid. "Clear" as used here is a relative expression only, representing normality; the water always contains a fine suspension of detritus, and is never "crystal clear".

The actinic value of the *light* at the time of the rise was measured on a Wynne sensitive-paper meter. These measurements are only very approximate, as this type of exposure meter is of little practical value at this time of the day.

The *hatch of "fly"* was noted as 0, few, moderate or good; a considerable personal factor is involved here, as means were not used for accurately estimating the number of "fly". The species of "fly" seemed to possess no particular importance. From April till the end of May, the "flies" were almost exclusively a large species of Chironomids, the cast cuticles of which floated abundantly on the water. Small Chironomids comprised the later hatches, and throughout the period from May to July small numbers of Ephemerids augmented the evening hatches. *Sialis*, Plecopteran and dragonfly imagos take little part in the hatches concerned, owing to their habits. The majority of "flies" appeared late in the afternoon and were often thick on the water some time before the rise commenced.

Thundery weather was noted, the writer being about as sensitive as the average person to the "closeness" of the atmosphere.

The *maximum and minimum temperature* during the preceding 24 hr., together with the water temperature at the time of the rise were recorded by a mercury recording max.-min. thermometer (° F.) suspended in about 10 in. of water 5 ft. from the shore. No marked difference was noted between temperatures taken at this spot and those recorded occasionally in mid-lake.

The *barometric pressure* and *phases of the moon* were noted. All the data were taken in the evening at the commencement of the rise. Fortunately the weather during the two years' observation was "mixed", and the influence of the various factors could be readily assessed.

5. Observations

Temperature. The correlation between the water temperature and the quality of the rise is very striking. In the detailed graphs, 1937 results only are plotted, since results for 1938 are essentially similar. In fact, temperature (or conditions immediately dependent on water temperature) appears to be the most important single factor determining the nature of the rise.

Other conditions being favourable, temperatures constant between a maximum of 56–61° F. and a minimum of 52 57° F., or a marked fall of temperature after a high temperature period, were invariably followed by good rises, or an improvement on the previous rise. The period April to the second week of May 1937, was marked by the low water temperatures and good rises; from May onwards the water became progressively warmed up and the rise deteriorated in quality. A marked fall of temperature at the beginning

Table 1. *Summary of results*, 1937. *Number of rises in different classes, in different conditions*

Weather	0	Sporadic	Poor	Moderate	Good	Total no.
Wind:						
N.	0	0	0	0	0	0
N.E.	1	0	1	0	3	5
E.	0	0	0	0	0	0
S.E.	0	1	0	1	3	5
S.	0	0	1	3	1	5
S.W.	4	6	1	5	0	16
W.	2	3	2	3	1	10
N.W.	0	1	1	1	0	3
0	13	16	2	0	4	35
Variable	1	5	2	4	3	15
Slight	4	5	3	8	5	25
Good	2	2	1	1	0	6
Sky:						
Clear	4	8	0	5	4	21
Few clouds	3	6	2	2	1	14
Cloudy	3	2	2	3	5	15
Overcast	7	10	4	3	2	26
Heavily overcast	2	0	0	0	0	2
Surface:						
0	14	18	2	7	5	46
Slight	4	4	2	3	4	17
Medium	2	4	4	3	2	15
Misty	5	8	0	1	2	16
General weather:						
Cold	1	1	4	1	2	9
Mild	7	10	4	8	10	39
Warm	11	15	0	4	0	30
Dull	6	5	4	1	3	19
Occasional sun	3	10	3	7	5	28
Sunny	10	11	1	5	4	31
Rain:						
0	12	22	7	11	12	64
Slight	4	3	1	2	0	10
Medium	1	0	0	0	0	1
Heavy	2	1	0	0	0	3
Water:						
High	4	8	3	6	0	21
Normal	10	9	3	1	0	23
Low	2	6	0	3	1	12
Clear	12	18	3	8	1	42
Cloudy	1	5	1	2	0	9
"Fly":						
0	6	0	0	0	0	6
Few	5	8	6	4	1	24
Moderate	5	13	2	0	1	21
Good	2	5	1	9	8	25
Rain in day	9	6	3	3	2	23
Thundery	7	2	0	1	0	10
Temp. max.:						
50–55° F.	2	2	1	0	0	5
56–61° F.	2	3	5	3	7	20
62–67° F.	5	4	1	8	4	22
68–73° F.	5	17	1	2	0	25
74–79° F.	5	1	0	—	0	6

Table 1 (*continued*)

Weather	0	Sporadic	Poor	Moderate	Good	Total no.
Temp. min.:						
46–51° F.	3	3	1	2	4	13
52–57° F.	2	4	6	4	7	23
58–63° F.	9	15	1	6	0	31
64–69° F.	5	5	0	1	0	11
Barometer:						
29–29·5 in.	2	0	2	0	1	5
29·5–30 in.	15	22	6	11	7	61
30–30·5 in.	1	2	0	2	4	9

Total no. of observations ...	78
Total no. of good rises ...	12
Total no. of moderate rises ...	13
Total no. of poor rises ...	8
Total no. of sporadic rises ...	26
Total no. of 0 rises	19

of June, and a less marked fall at the end of June resulted in distinct improvements on the quality of the rise.

The influence of temperature in determining the type of rise is clearly shown in the frequency curves of the types of rises (Figs. 2, 3). Fig. 2 shows how maximum temperatures of 56–61° F. were accompanied by good rising, 62–67° F. by moderate rising, and 68–73° F. by sporadic rising. It is significant to note that poor rising was most frequent at temperatures favourable to good rising, and it appears that such poor rising is the result of limiting factors, later to be discussed, which may operate when conditions otherwise are favourable for good rising. Similarly 0 rise is not dependent on temperature, but on inhibiting factors which may operate regardless of temperature.

A similar, though not so convincing, result is evident using minimum temperature as abscissae (Fig. 3). It would appear, however, that within the limits observed (46–69° F.) the minimum water temperature is not so important as the maximum temperature reached during the day, a result which would be expected within summer ranges, when the temperature does not fall sufficiently low to affect the feeding of the trout.

Range of temperature does not appear to be important, though the majority of good rises took place when there had been 8° F. or more difference between the preceding maximum and minimum temperatures; nor does the water temperature at the time of the rise (within the limits of the range however) appear to be significant.

The mode of action of temperature in conditioning the rise is not obvious. Teleost fish in general appear to be very sensitive to slight differences of temperature (Bull, 1936; Chidester, 1924; Gurley, 1902; Ward, 1927; Wells, 1914). Certain marine fish respond purposively to increases of temperature as slight as 0·03–0·10° C. (Bull), and it has been stated that a difference of 1° F. may determine the choice of two streams by migrating salmon (Ward), though this requires confirmation. It is not surprising therefore that trout

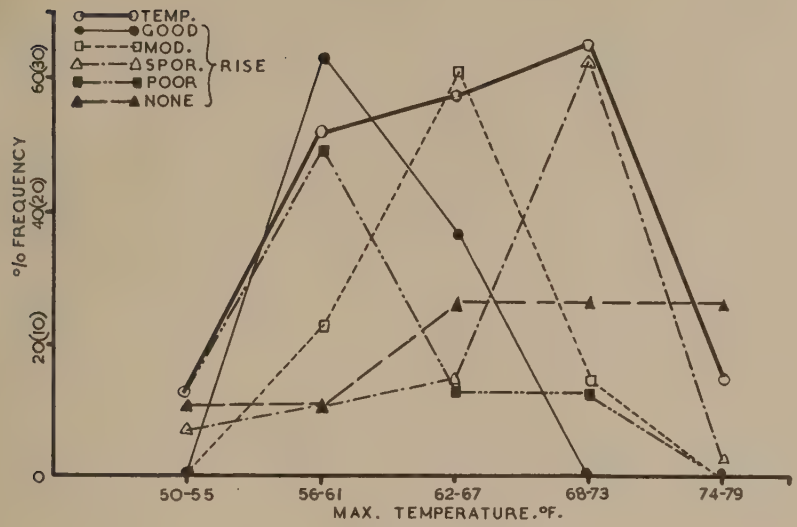
TEMP.
GOOD
MOD.
SPOR.
POOR
NONE
RISE
% FREQUENCY
60(30)
40(20)
20(10)
0
50-55
56-61
62-67
68-73
74-79
MAX. TEMPERATURE. °F.

Fig. 2.

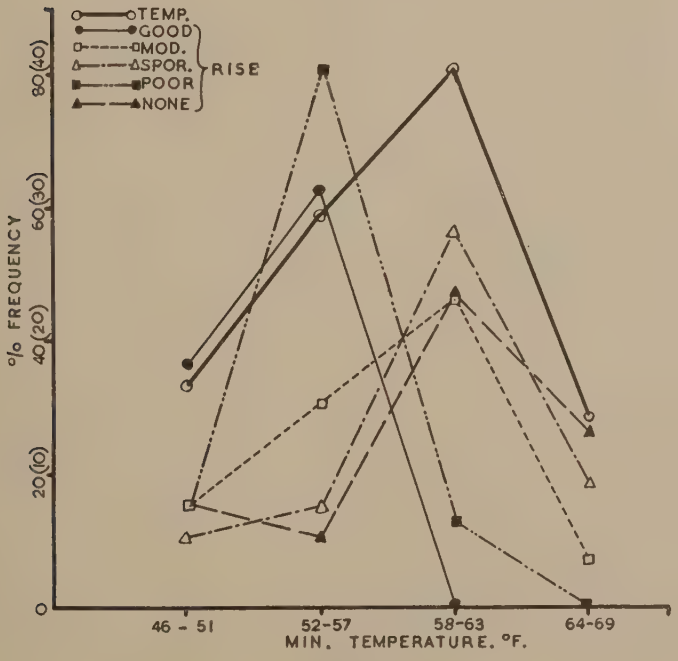
TEMP.
GOOD
MOD.
SPOR.
POOR
NONE
RISE
% FREQUENCY
80(40)
60(30)
40(20)
20(10)
0
46 - 51
52-57
58-63
64-69
MIN. TEMPERATURE. °F.

Fig. 3.

respond in degree of activity to such relatively large seasonal and diurnal variations. High temperature exercises a very distressing effect on trout; Gardner & Leetham (1914*a*, *b*) record the instance of trout, which, placed in fully oxygenated water at 25° C. (77° F.), exhibited every sign of distress, which was not due either to asphyxiation or sudden change of temperature.

Increase of temperature results in increase of rate of most physiological processes such as respiration, heart beat, enzyme action and metabolism, up to a certain limit. In addition the daily food requirement is greater in warm water, hence hunger cannot be an important factor in rising. It seems as if high water temperature in some way makes the fish lethargic, and since fish are poikilothermic and hence largely dependent on external temperature for body temperature, this change would be emphasized. Menzies (1936) has suggested that "temperature may play an important part in encouraging trout to feed or in limiting their opportunities of so doing. When the water descends to within a few degrees of freezing point they become quiescent and may refuse to take any food at all, while, on the other hand, when the immersed thermometer rises above 70° F. the food may also become distasteful to them".

The relation between rise and temperature is not absolute but progressive. A sudden fall of temperature is not immediately followed by a good rise: there is a time lag of a day or so, provided the temperature does not immediately rise again (as on 29 May–5 June). Conversely, a period of steady high temperature is not followed by a sudden deterioration in the rise, but results in a slow deterioration (as on 30 June–20 July). These time relations between fluctuations of temperature and differences in rising suggest that some other factors dependent on temperature, but slower in action are involved; and the amount of dissolved oxygen suggests itself as a possible factor.

Unfortunately no oxygen determinations could be made, but reasons have been given to suppose that in such a lake there is a relative progressive diminution in dissolved oxygen as the season advances. If so it would appear that diminution of oxygen may play a large part in conditioning rising activity by progressive respiratory difficulty and consequent lethargy. This would explain the observed time lag, since aeration of such large masses of water is a relatively slow process, and a sudden fall of temperature results in only slowly increased aeration due to photosynthesis by plants, surface diffusion, and surface water agitation.

Trout have a higher dissolved oxygen minimum than most other freshwater fish (Welch, 1935), and though it has been shown that the O_2 consumption is independent of the O_2 tension in the external medium for the greater part of the normal range (Keys, 1930; Washbourn, 1936), yet the O_2 absorbed is a function of the temperature, and the O_2 consumption of trout is almost doubled for a rise of 10° C. in the external medium. In addition, the O_2 consumption is varied by the metabolic rate and activity of the fish, and since at a higher temperature trout require more O_2, more work must be done by

the respiratory mechanism to obtain it (Gardner & Leetham, 1914*a*, *b*). The asphyxial condition is reached within quite small limits of O_2 tension, and is reached at higher limits of O_2 tension at higher temperatures. Low O_2 tensions cause distress in respiration and behaviour (Gardner & Leetham).

Trout use more O_2 per kilo per hour than other freshwater fish, and the asphyxial limit of O_2 tension is much higher than for roach. On many nights when the trout rise was sporadic, the roach in the lake would be rising freely. Furthermore, the O_2 consumption is approximately proportional to the body weight, and on nights when the rise was sporadic it was noticed that the smaller trout would constitute the major part of the rises, larger fish usually leaping right out of the water as if in respiratory difficulty. Sporadic rises also were due usually to the same few fish rising each time.

In flowing waters, though diurnal variations of oxygen have been recorded (Butcher *et al.* 1927), oxygen diminution is never strongly marked, the water remaining sufficiently saturated even at high temperature owing to continuous agitation; and even on warm summer days trout may rise freely on a river or stream.

Coupled with the fact that O_2 tension of water is directly proportional to the temperature of the water, these data indicate very strongly that O_2 tension, in addition to a direct effect of temperature, constitutes perhaps a very important factor in conditioning the rising activity of trout. This has been suggested previously by several anglers, including Allan (1936), and Mackeachan (1923).

Allan (1936) and Chrystal (1927) describe two instances when trout, which previously were not rising, rose freely during a sudden snowstorm. While this is, in my personal experience, certainly not a constant phenomenon, it is nevertheless interesting in view of the effects of temperature described above. While the trout may have been rising *at* the snowflakes, it is very likely that the sudden lowering of the surface water temperature stirred the fish into rising actively, as Allan suggests, assuming there were sufficient flies on the water. It is improbable however that O_2 tension of the water could be so suddenly increased by snowflakes as to affect the trout, as Allan further suggests.

Wind. Wind is the most important factor in increasing aeration of lake water by surface agitation, but in this study the majority of good rises took place when there was no wind or slight north-east or south-east wind. Possibly wind has no effect on this lake, as it never reaches sufficient force to break the surface into waves. Wind may reduce the water temperature however and improve the rise (3 and 4 July), but strong winds from any quarter at the time of the rise are usually detrimental, because they drive the flies off the water (5 April, 22 May).

Most anglers find east winds detrimental to rising, but these are probably east winds of considerable velocity and typical "biting" nature. East winds

on this lake are never strong or very cold owing to the surrounding trees, and are usually prevalent in the early part of the year when water temperatures are favourable for rising. Strength of wind appears to be more important than direction.

Sky. The state of the sky appears to play only a minor part in determining the quality of the rise, though a cloudy sky appears to be more conducive to good rises than a clear sky; the latter state is more frequent with moderate rises. Possibly the sky has more effect on day rising.

Surface. The state of the surface appears of little importance in influencing the rise, though of course it depends on the strength of the wind. However, a misty surface almost invariably results in poor or sporadic rises, this being due to the mist driving the flies off the water and bringing hatch of fly into play as a limiting factor. The occcasions when moderate or good rises were recorded with a misty surface were those when the mist did not blanket the whole surface water, but was distributed in local patches near the edge of the lake.

General weather. The weather during the day is important only in so far as the air temperature and duration of sunshine affect the water temperature and oxygen content. Sunshine naturally is favourable for photosynthetic production of oxygen, but this beneficial effect is probably negatived by prolonged sunshine and consequent raising of the water temperature accelerating the processes reducing the oxygen content of the water.

Table 2 shows that warm, sunny days are accompanied by 0 or sporadic rises; mild days with occasional sun favoured good or moderate rises. Poor rises followed mild or cold, dull days, the poor hatch of fly probably accounting for this.

Rain. Rain at the time of the rise is definitely unfavourable; whether slight, medium or heavy it results in no or sporadic rises. This is apparently a purely mechanical effect in driving the flies off the water and thus limiting the rise.

Rain during the day may have either of two opposite effects. If it is heavy during the season of the year when water temperatures are already favourable, it results in a deterioration of the rise (27, 28 April, 9, 22 May), apparently as a result of limiting the hatch of fly. Slight rain in the day during this period has little effect (7, 11 May). Later in the season, however, when water temperatures are high and the fish sluggish, rain during the day exercises a beneficial effect, probably by cooling the water (29, 30 June, 9, 19 July). Slight rain again has little effect. Rain during the day during this warm period does not appear to have the same limiting effect on the hatch of fly as earlier in the year, perhaps because different species of fly are emerging at that time.

Thunder. These results bear out the observation so commonly recorded that the imminence of thunder or a thundery atmosphere exerts a very definite

Table 2. *Conditions favourable for each type of rise*

Good	Moderate
N.E. or S.E. wind, slight or none	S.W. wind, slight
Cloudy sky	Clear sky
Slight ripple	No ripple
Mild, occasional sun	Mild, occasional sun
No rain	No rain
High water(?) (no observation)	High water
Clear water(?) (no observation)	Clear water
Good "fly"	Good "fly"
Perhaps rain in day, no thunder	Perhaps rain in day, no thunder
Maximum temperature 56–61° F.	Maximum temperature 62–67° F.
Minimum temperature 52–57° F.	Minimum temperature 58–63° F.
Barometer 29·5–30 in.	Barometer 29·5–30 in.

Poor	Sporadic
W. wind, slight	S.W. wind or 0
Overcast sky	Overcast sky
Medium ripple	No ripple
Mild or cold, dull	Warm and sunny
No rain	No rain or rain
High or normal water	Normal water
Clear water	Clear water
Few "flies"	Moderate "flies"
Perhaps rain in day, no thunder	Perhaps rain in day, and thundery
Maximum temperature 56–61° F.	Maximum temperature 68–73° F.
Minimum temperature 52–57° F.	Minimum temperature 58–63° F.
Barometer 29·5–30 in.	Barometer 29·5–30 in.

0
S.W. wind or 0
Overcast sky
No ripple
Warm and sunny
No rain, or slight or heavy
Normal or high water
Turbid or clear water
Moderate or 0 "fly"
Rain in day and thundery
Maximum temperature 62–79° F.
Minimum temperature 58–63° F.
Barometer 29·5–30 in.

inhibiting effect on the trout. Though, as Mackeachan (1923) and other writers have observed, trout will rise freely *during* a thunderstorm, the period *before* a thunderstorm is unfavourable for rising.

The mode of action of such electrical states on fish is quite obscure; certainly many people feel disinclined to exertion in thundery weather, but this is due partly to high humidity, unrelieved by movement of the air, which would seem of no obvious importance to fish. Allan suggests that east winds may have the same detrimental effects by virtue of the fact that polar winds (which become easterly in direction due to the land masses and the revolution

of the earth) have been supposed to be more highly charged electrically than other winds.

On 23 May 1937 thundery weather was recorded, but the rise was unaffected; in view of the other very positive findings this remains unexplained.

Barometric pressure. The atmospheric pressure itself appears to be unimportant, except in so far as it indicates other weather conditions. The majority of good rises occurred when the pressure was falling slowly, but this is not a constant effect, nor is the converse true.

Water conditions. Water conditions were unfortunately not recorded during the early part of the investigation. Low water is however an accompaniment of warm weather and high water temperatures, and is consequently characterized by no or sporadic rises. Water level falls progressively as the season advances, and the heights recorded as "normal" were therefore obtaining when the rise was deteriorating. It is probable that high water would have been recorded during the season of good rises. Exceptionally high water, such as on 12 and 13 May, the result of a very heavy thunderstorm on the 12th, resulted in no rise at all; the water was very turbid, and the amount of suspended detritus appears in some way to affect the hatch of fly.

Small rises of water level as on 29, 30 June and 19 July were followed by improvements in the rise, but this is probably a condition incidental to the lowering of the water temperature, since the rise in level on 15 July was not accompanied by lowering of water temperature not an improvement in the rise.

In flowing water rise in water level appears to stimulate the trout to feed on *underwater* food which becomes more available; such a result may occur in standing water, though rising water would not make the food more available by dislodgment or migration, except in the littoral region (Moon, 1935).

Hatch of "fly". Other conditions being favourable, hatch of "fly" undoubtedly acts as a limiting factor. Apart from inherent specific tendencies determining the length of larval life, different species of "fly" emerge at different seasons, but little is known of the factors controlling the emergence of the imagos, though mean temperature itself probably plays a large part in determining at what time during a period of days or hours the imagos will emerge.

Several factors appear to exert their effect on the rise by reducing the number of "flies" on the water, e.g. rain during the rise, mist, and strong winds. The effect of these conditions on the "flies" which emerge is easily demonstrated by the behaviour of the swifts and bats which hawk several feet above the water under such conditions, instead of skimming the surface as on favourable evenings. These factors may diminish the rise by driving most of the "flies" off the water (27 April, 9, 19 May and others) or reduce it to 0 by driving all the flies off the water (28, 29 April and others). Factors other than these may affect the rise through hatch of "fly", such as the amount of suspended detritus, or the amount of sunshine. For example,

29 April showed little change in water temperature, but was a cold, dull day and no hatch of "fly"took place.

Fig. 3 shows the percentage frequency of type of rises plotted against abundance of "fly", though the curves are not typical because hatch of "fly" was not measured in an exact manner. Nevertheless it is clear that good and moderate rises have their maximum frequency with good hatches, sporadic rises with moderate hatches and poor rises with few "flies", limited in number by one or more of the above factors. While 0 rise is most frequent with 0 "flies", 0 rise may result when "flies" are few, moderate or good, owing to

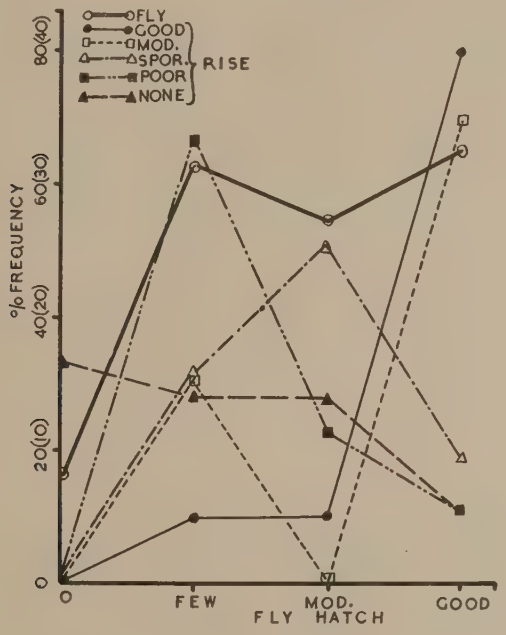

Fig. 4.

the operation of inhibiting factors such as the imminence of thunder. Hatch of "fly" deteriorated as the season advanced, but in general it appeared sufficiently abundant to support a good rise had the conditions been favourable.

Light. Light is almost certainly the factor which controls *when* the fish will rise, other factors determining *if* the fish will rise. The regularity of the evening rise is a very striking feature; it starts at almost the same time each evening after sundown and hence is later in the evening as the days lengthen. Fall of water temperature after sundown is not important, as on several occasions the water did not fall from the day's maximum until 2 or 3 hr. after sundown. It is a curious fact that the rise starts at the same time after

sundown irrespective of whether the sky is clear or overcast. If trout were susceptible to visible light as we perceive it, we would expect the rise to start somewhat earlier on cloudy or overcast evenings.

Light enters the water from two sources, direct light from the sun and reflected light from the sky. True twilight does not occur under water (Ward & Whipple, 1918), direct light from the sun being totally reflected as soon as the sun sinks below a certain angle. Hence the onset of darkness is comparatively sudden on water, the very short twilight being provided by reflected light from the sky, which may be only slightly less intense in cloudy weather.

The trout may perhaps be relatively insensible to the differences in value of reflected light from the sky. Allan has suggested that trout may be dazzled by strong sunlight, and hence rise more freely on dull days, though this is from personal experience not confirmed, as I have seen good rises on sunny days. It may be, on the other hand, that trout may appreciate the longer infra-red rays which can penetrate cloud and fog up to a certain limit. These longer wave-lengths penetrate farther in cloudy or turbid water than the short blue rays, owing to a more rapid relative absorption of the latter by suspended particles; and are least deflected on refraction. Trout certainly appear to have a particular appreciation of red as such, and the addition of a red or partly red artificial fly to a cast may improve a day's fishing beyond question.

Phases of the moon. These appear to be of no importance, even over two years' observation period. The effect of moonlight, however, has not been studied.

6. Discussion

Conditions accompanying the various types of rises are summarized in Table 2, those being the conditions prevailing in the majority of occasions when each type of rise occurred (Table 1). These form a combination of conditions "ideal" for each type of rise and were seldom realized completely on any one occasion. It appears that combinations of factors are more important than any one factor, though any one factor may at times become limiting in its action. Possibly also *change* of conditions plays some part in influencing the rise.

It is not certain how far these determining factors control day rising, though almost certainly they are concerned, since the same change of behaviour is involved. This study reveals under what conditions rising is likely to occur, and the habit itself has been suggested as originating in a psychological "drive". Such a study would not be easy on large bodies of water or in flowing waters, because these environments are relatively more constant in their physical and chemical characteristics. Small bodies of water such as that under consideration are subject to more noticeable changes and rapid

variation of conditions, rendering it more easy to separate and assess the various factors concerned.

However, the trout themselves probably exhibit physiological differences in standing and flowing water. Washbourn (1936) has shown that trout fry from swift-running water have a higher metabolic rate than those from slow-running water; it is probable therefore that trout from any flowing water have a higher metabolic rate than those from standing water. These facts should be taken into consideration when attempting an explanation of rising in rivers, for example, since the effect of various conditions would be accentuated or decreased by the differences in metabolic rate of the fish.

Allan suggests that concerted rising may be due to "imitative" actions of one trout by another, but in view of the scarcity of knowledge concerning fish psychology, this must be considered reservedly. Indeed, in view of the apparent conditioning of fish behaviour largely by environmental stimuli, there is little reason to see why the individuals in a group of fish under similar conditions should not show the same response to certain combinations of external stimuli, at the same time, without involving endogenous "imitative" processes.

In conclusion I wish to express my grateful thanks to Mr Herbert C. Gaze for permission to study and fish the lake; and to Mr R. Haslam of the Mill House, Wonersh, for information and permission to use his land. Mr W. J. M. Menzies, Chief Inspector of Salmon Fisheries for Scotland, was always ready with helpful criticism and advice; while I owe a great deal to the co-operation of my father.

7. SUMMARY

Rising of trout involves a change in behaviour which appears to be conditioned largely by external environmental factors, though the habit itself probably originates in a psychological "drive" to seek food.

The factors conditioning the evening rise of trout were studied on a small freshwater lake, the physical and ecological features of which made it subject to sudden and marked variation of conditions. Observations were made every day during late spring and early summer for two years. Temperature, or conditions immediately dependent on temperature appear to be the principal factors controlling rising; high temperatures cause the rise to deteriorate and low temperatures are favourable for good rising down to certain limits. In addition to a direct effect of temperature, the trout appear to be influenced in rising by the O_2 content of the water, being (within certain limits) most active when the O_2 content of the water is high and the temperature low. This combination of factors operates most markedly in standing waters, since in flowing waters oxygen content is probably always sufficiently high.

Hatch of "fly" acts as a limiting factor, other conditions being favourable; strong winds, mist on the water, rain at the time of rise and perhaps turbidity

of the water all have an adverse effect on rising by limiting the hatch of "fly". When other conditions are unfavourable, rain during the day has a beneficial effect, probably by cooling the water and raising the O_2 content; it has an adverse effect when other conditions are favourable. A thundery atmosphere is invariably detrimental to rising, but its action is obscure.

Direction of wind, surface ripple, state of the sky, barometric pressure, and phases of the moon all appear to be unimportant in themselves, at any rate in this study.

Light is the most important factor determining *when* the trout will rise, other factors determining *if* the trout will rise. Since the evening rise commences at the same time after sundown irrespective of the state of the sky, it appears as if trout are relatively insensible to the smaller differences in light value, or else are sensitive to longer wave-lengths such as infra-red.

Combinations of factors are more important than any one factor in influencing the rise, though any one factor may become limiting in its action. Day rising of trout is probably influenced by the conditions described, but trout from different environments are known to exhibit physiological differences which may modify to a greater or less degree the action of such environmental conditions.

Abbreviations and symbols used in graph

Wind. Arrows fly with the wind, centre top being north.

Wind strength. Circle outside sky symbol = 0, opposite feathers = variable, 1 feather = slight, 2 feathers = good.

Sky. Clear circle = clear, 2 vertical lines = few clouds, 3 vertical lines = cloudy, 4 vertical lines = overcast, 4 vertical lines and 1 horizontal = heavily overcast.

Surface. 0 = calm, S = slight ripple, M = medium ripple, T = misty.

General weather. C = cold, M = mild, W = warm, D = dull, O = occasional sun, S = sunny.

Rain during rise. 0 = no rain, S = slight rain, M = medium rain, H = heavy rain.

"*Fly*". 0 = no flies, F = few flies, M = moderate hatch, G = good hatch.

Moon. F = full, N = new.

Rain in day. Round black dot.

Thundery. Square black dot.

Water. C = clear, D = cloudy, T = turbid.

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INSECT OUTBREAKS IN EUROPE[1]

By J. RICHARD CARPENTER

(*With* 11 *Figures in the Text*)

E.M.N.

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1. Introduction

This study is the natural outcome of a series dealing with fluctuations in the numbers of insect populations over various periods of time: throughout the periods of the day (Carpenter, 1935, 1936), and throughout the seasons of the year (1935, 1937). It represents an attempt to bring together some of the voluminous data pertaining to the recorded insect outbreaks of Europe and to treat them as normal fluctuations in population numbers and hence make them comparable with the studies done on insects during periods of much shorter duration, as well as with those done on other elements of the fauna (mostly mammals and birds) and flora (e.g. tree-ring studies). There has been little attempt to enter into the phenomenon of the insect outbreak as such; the reason that insect outbreak records have been used is that they are the only indices we have of long-period fluctuations in insect numbers. Little work has been done on fluctuations in communities as entities over long periods, partly because of the complexity of the problem, and partly because of the viewpoints of the investigators who have been, for the most part, interested only in individual species.

[1] Fluctuations in Biotic Communities, 4.

Most of the work on fluctuations of animal populations has been done on vertebrates (chiefly mammals and birds), although some workers have been studying fluctuations in individual species of insects. There exists in the literature, however, a rich supply of data concerning not the actual *numbers* of insects present at any one time, but the *times* during which they have been abundant: in popular parlance, "insect outbreaks".

In this investigation insect outbreak records have been used as indices of fluctuations in insect populations. While in most cases there are no figures available relating to the actual numbers of insects present at any given time, it is obvious that many more individuals are usually present under "outbreak" conditions than during "normal" or non-outbreak years. Thus, a rough approximation to the years when the total populations of insects were greater may be found in the study of the years when these outbreaks occurred. It is not the purpose of this study to go into the actual causes, nor the methods of preventing, outbreaks: such would be far beyond its scope. It is, however, hoped that in attacking the problem of outbreaks as a whole from a new angle—that of considering the individuals of all species of a large area as members of one population—some light may be thrown on the outbreak problem.

What, exactly, is an outbreak? Anyone familiar with the entomological literature will immediately recognize the different points of view symbolized by the German *Auftreten* and *Kalamitäten* ("*Massenphänomen*" according to Friederichs, 1930, *Gradation* according to Börner and his associates), the French *Invasion*, the Russian *Massovie*, and the English *Outbreak*. One finds everything from new introductions of isolated individuals to periodic migrations of swarms of locusts, from small "outbreaks" in market gardens and greenhouses, and records concerning cutworms and the like (albeit they may have been abundant for some time) brought to notice when a given area is ploughed, to the appearance of the periodical *Melolontha* or *Cicada*—all termed "outbreaks". (The concept of an outbreak for the purposes of this paper will be given below. Other examples of so-called "outbreaks" may be found for places where burning and other disturbance of nearby areas causes local increases, e.g. Prof. J. Munro tells me that *Strophosomus lateralis* increased in numbers in Sussex pine plantations when the grass of the plantation area was burned.) With such a vagueness as a background, it is small wonder that only rather recently has any real attempt been made to understand the actual functioning of insect fluctuations. The detailed investigations of Eidmann (1934) and Schwerdtfeger (1935) are examples of this work on forest insects in Germany, as is that of Barnes (1936, on the gall midges (Cecidomyidae) in Britain, and Evans (1933, 1934), Wheeler (1934) and Andrewartha & Steele (1934) on thrips in Australia. These papers should be consulted for the exact details of the fluctuations and the numbers of individuals present in various recent years for *Panolis*, *Bupalus*, *Dendrolimus*, *Sphinx*, *Cecidomyia* and *Thrips imaginis*.

The earlier compilations of insect outbreak records were made following the great locust invasions of the middle seventeenth century; this type of work continued throughout the eighteenth century and up to the present time. (For a guide to this voluminous literature see Mann's (1879) bibliography, which is a *cade mecum* to the more important works of reference in this subject published before 1878. The more important papers since are those of Keppen (1870), Swinton (1883), Trinchieri (1916), Kulagin (1921), Rudy (1923), Rethley (1925) and Zverazomb-Zubovskiĭ and others (1926).) One of the first compilations of records for insects other than locusts appeared in J. F. Krebel's *Forst- und JagdKalendar für das Jahr* 1802, where there were listed the years of "Raupenfrass" (larval attack) back to 1449. After 1826 there were published a number of papers dealing with the periodical appearance of many insects. In 1855 Assman attributed these appearances to meteorological causes; this resulted in a certain amount of controversy in the literature and in the attempted correlation of fluctuations and outbreaks with sunspots. Keppen (1870) and Swinton (1883) were others among the earlier proponents of this idea, a subject still actively pursued. However, no entirely satisfactory positive correlation between sunspots and periodic biotic phenomena has yet been shown.

The more recent movement of compiling lists of insect outbreaks other than those of locusts was apparently initiated by Beck in 1910. He was followed by Kulagin (1913) who presented an account of the more important pests of the provinces of European Russia for the period 1892 1912; in a subsequent paper (1934) a more detailed list for the Moscow region during the period 1870–1933 was published by the same author. In 1925 Averin published a short graph of insect abundances in Ukraine for the period 1910–25. In Germany this movement has been very noticeable, particularly with reference to forest insects; names which should be mentioned in this connexion are Keler, Gasow, Ritter, Schnauer and Wilke; and for China, Hsu. Following this compilatory period, and partly coincident with the latter portion of it, came the time when work was done on the range, numbers, diseases, and control of individual species.

Several government boards of agriculture have followed the examples set by the early compilers, and government reports are now available for the more injurious insects in their respective areas; though, because of the vagueness of the reports, they are frequently difficult to use. A desirable addition to the usual kind of recording would be to take into account the regional factors possibly causing the outbreaks. For example, ecological "vegetation" regions could be used to great advantage in Russia, Germany, and the United States; climatic regions are another possibility. The importance of regional differences in the consideration of outbreaks has been pointed out by Cook (1929) who found from his study of the armyworm (*Cirphus punctata*) in America, that five states had many more outbreaks than the others. Other advocates of this

principle are Schwerdtfeger and Friederichs. This principle has, according to Shchegolev (1935, 1936), been adopted by the Russian administration, although no maps or definite plans are given in his report. In the present analysis, ecological biotic community areas have as far as possible been used for analysing and presenting data. Some of these government reports require comment here.

England and Wales. Reports (of varying title) have usually been issued every two or three years since 1917 by the Ministry of Agriculture and Fisheries, London. Species undergoing outbreak were formerly given under the type of food plant; this caused much duplication of listing. Such duplication, however, probably indicates to some extent the intensity of outbreaks. Comment on the extent of the region infested is usually added. More recently notes have also been made for some species as to whether they appear to be more or less abundant than usual, and whether or not the numbers of individuals appear to be on the increase or decrease in different areas. There is usually an index of species at the end of each report. England and Wales were at one time divided into 14 districts for reporting purposes, but these have not been frequently mentioned in the later reports. A list of the usual plant pests was given in 1928 (Appendix 2, *Minist. Agric. & Fish. Misc. Publ.* No. 62) but is in need of revision.

Poland. The Polish report for 1919–30 (Ruskowski, 1933) has species listed according to field crops, garden crops, decorative plants, forests and granaries, with the initials of the 15 collaborators given for each outbreak reported from their respective districts. There is an index which is not without errors, but which aids in discovering the species desired. (See Kuntze, 1936, for correction of Coleopteron names and certain other revisions, before using this paper.) There is one great disadvantage in using this work: it is apparent as soon as the book is examined closely that there are many more outbreaks recorded in the latter portion of the period under review than in the earlier years. One is forced to the conclusion that the bureau, which was created at the end of the war and with the establishment of the Polish government, grew more efficient as time went on, and that the same degree of observation was not used throughout the entire period covered by the report.

Germany. The German reports are given in the *Nachrichtenblatt für den deutschen Pflanzenschutzdienst*, published by the Biologischen Reichanstalt für Land- und Forstwirtschaft, Berlin-Dahlem, with frequent maps for the abundant species of insects, showing areas where there are different degrees of infestation. There is usually a yearly conspectus in December or January. The small territorial areas reported make the reports difficult to use. The yearly publication, *Bibliographie der Pflanzenschutzliteratur*, from the same institution, was not used in the compilation of the data for this study, but would be useful in more intensive studies.

The *Review of Applied Entomology*, a British publication, reviews the world

literature about pest outbreaks and preventive measures. Its abstracts, although very useful, are usually too short to give an adequate account of the details of the outbreak, but do give notice of the existence of a publication dealing with the subject. Nearly all of the publications reviewed may be consulted at the library of the Imperial Institute of Entomology in London.

For source material I have gone through the *Review of Applied Entomology* (Agricultural section) from 1913 (vol. 1) to 1935, and selected for further examination all papers which appeared to report on outbreaks. Some other titles have been added by the perusal of bibliographies in the papers thus found, and by searching through various promising publications. The list is probably not complete, but it is believed to be nearly so, and it supplies a sufficient record for the more important outbreaks in the period since 1800 at least to enable some conclusions to be drawn. Since most of the source material has been referred to in the *Review of Applied Entomology*, the reader is directed to it for the many references not given in the present bibliography.

2. The concept of an outbreak

The concept of an "outbreak", as we have seen, is rather vague in practice; the term is taken for granted by most agricultural entomologists, and the only definition which I have been able to find which is in any way applicable is that of the *Century Dictionary*: "a sudden and active manifestation"—a fairly vague definition. For the purposes of this study an outbreak will be considered as the time during the fluctuation cycle of an insect (or other animal) when it is abundant or injurious enough (or both) over an appreciable area to warrant a record being made by observers. (It is realized that outbreaks due to local disturbances—fires, etc.—cannot be attributed to "natural" population increases.) More will be said about the nature and possible causes of outbreaks in the final section. Something is said about true "invasions" (English sense) in section 5 (*b*).

Since one of the hypotheses underlying this study is that the biotic community reacts as a whole to its environmental conditions, the analysis of data is made with this in mind. According to this idea we may expect a general reaction of an ecological population on any area to its environmental conditions. If, instead, each species-population reacted in its own way to its environment, one might well expect a similar number of outbreaks (i.e. peaks of fluctuation cycles) every year, but, as we shall see, this is rarely the case. In making such a study, the actual number of animals per acre or other unit would be the ideal measure of fluctuations and their rate of change; however, with the data at hand this is not possible. But we do have the times when the various species-populations have been in excess of their usual numbers, which indicates the probable time of the "peaks" in their cycles. By totalling the number of these peaks (outbreak years) for each year over a given period we have a rough index of the state of the animal population of a given area.

At first it was thought that the number of reports concerning a given outbreak might be an index of its intensity, but this method was soon found to be impracticable. Therefore, for each area under consideration (and in the deciduous forest region the seven areas described below on p. 116) records of a single species in several localities within the area in the same year are considered as appertaining to the same outbreak; this method probably reduces as much as possible the errors due to non-recorded outbreaks and to those which have not come to my attention.

The present study includes outbreaks for the deciduous forest area of Europe, the other major ecological communities of European Russia, and the district of Hangchow, China.[1] These districts represent the most extensive recordings available, aside from those for the United States and Canada, which are not dealt with. In deciding which records were to go into each ecological area the following list of localities was compiled:

Arctic tundra (no records).

Taiga. North Russia, Finland, North Scandinavia, *Leningrad (=Petrograd, St Petersburg), Vologda, Kostroma, Viatka.

Deciduous forest (see list on p. 116).

Deciduous forest-steppe. Jugoslavia, Bosnia, Herzogovina, Albania, Bulgaria, *Ukraine, Saratov, Penza, Tambov, Voronezh, Kharkov, Poltava, Podola, Bessarabia, Simbirsk, Central Chernozem (black soil) Area, Orel (=Orlov), "Little Russia", Moscow (=Moskva).

Steppe. Hungary, Rumania, *Samara, Don province, Orenburg, Ekaterinoslav, Kherson, Tavrich (Tauriche), Crimea.

Semi-desert. *Tashkent, Astrakhan.

Caucasian forest area. *Stavropol, Dagestan, Kuba.

3. The European deciduous forest area

(*a*) *The vegetation*

The area of the deciduous forest of Europe, for which we have more insect outbreak data than any other region, is an area comprising most of the leading countries of Europe. The area has a temperate climate which is humid. The winters are relatively mild, the growing season not always being entirely interrupted: seasonal changes are more in terms of temperature changes than in rainfall. Precipitation is regular and well distributed, with a tendency towards a late autumn or winter maximum. The area is characterized by a regular occurrence of cyclonic storms.

The original vegetation (speaking historically) was dominated mostly by the broad-leaved hardwood deciduous trees after which the area is named. Beech and oak were perhaps the dominants over the greatest part of the area, having as abundant companions the maple, elm, chestnut, walnut, willow and poplar. The eastern limit of the beech is in Poland. At the northern

[1] Obtained from Hsu (1933). I am indebted to Mr Chu Yeng-Feng, formerly of Lincoln College, Oxford, for assisting me by translating parts of this report.

* Localities listed after the sign * in each division may be understood to be in the U.S.S.R. (with the exception of Bessarabia, included here since most of the records are pre-war).

border and on sandy soils near the central mountains there was a good admixture of coniferous trees as well. Close to the coast excessive humidity, a lower frequency of sunny days, and strong winds prevented the forests from

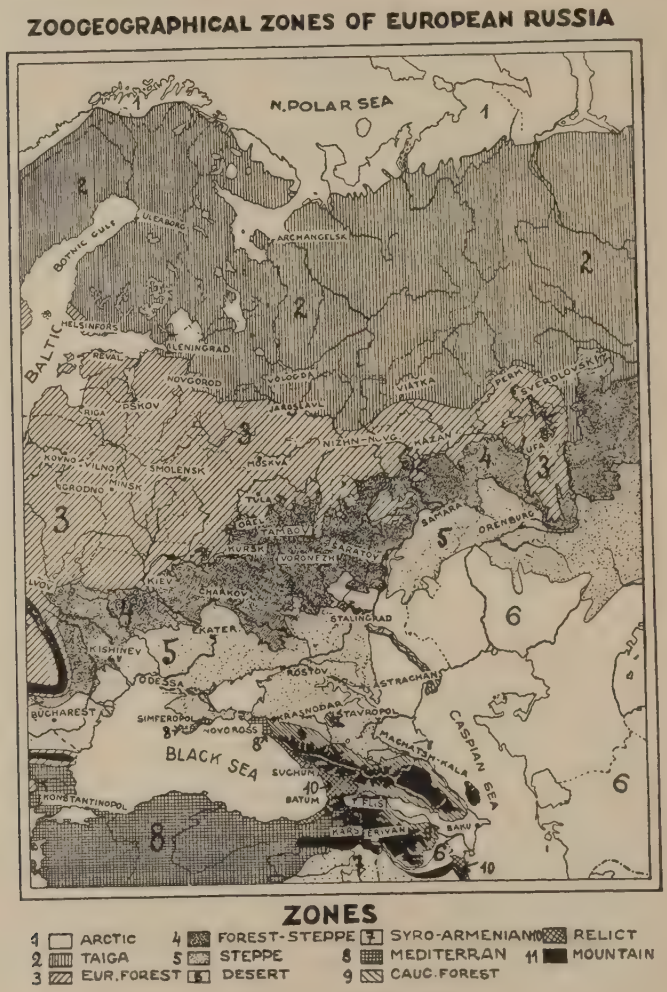

Fig. 1. From Filipev, 1929.

attaining their full development. The original forest is, of course, long since gone, and is to-day represented only by a few scattered relict patches.

At present nearly the entire area is given over to modern European methods of cultivation, grazing and some forestry. Of the many indigenous crops

grown, perhaps the most representative are the cultivated Brassicae (turnip, cabbage, rape), carrot, chicory, asparagus, sorrel, hop, forage grasses, pear, raspberry, strawberry, black currant and red currant. Many other now important crops have been introduced and their effect on the insect fauna must have been very important. The main insect problems are those concerning soil insects (wireworms, white grubs, Tipulids, etc.), forest insects (bark beetles, the nun, pine and tortrix moths, etc.), and the miscellaneous fruit and market-garden insects.

Fig. 2. Deciduous forest area of Europe showing subdivisions into which the general area was divided.

(b) Subdivisions of the area

In dealing with outbreaks in the deciduous forest area of Europe several things are at once evident: the detailed accounts furnished by the more recent government reports are very difficult to compare with the more casual earlier observations and, rather than throw the general survey out of proportion, there will be a separate consideration of them. The great expanse of the deciduous forest area and the bulk of its records made some sort of subdivision necessary. The plan here used is based more upon the amount of data available for the various regions of Europe than upon anything else, and no claims are made that a better analysis could not be devised. These arbitrary divisions are indicated on the adjoining map (Fig. 2) in which the following countries and areas are included in each section:

E. England and Wales, France (except the Riviera coast), Belgium, the Netherlands.

I. Germany (new political divisions) Gaue Bayern, Bayerische Ostmark and Franken, Sachsen, Thüringen, Baden, Schwaben; (old divisions) Baden, Würtemburg, Bavaria, Staat and Prov. Sachsen (Saxony), Thuringia, Anhalt, Kurmark, Altmark; Switzerland.

II. Germany (new) Rhineland, Saar, Pfalz, Südhessen, "Main-Rhein-Lahn-Fulda", Kurhessen, Westfalen, Unterwesen-Ems; (old) Westphalia, Rhine prov., the Hesse states, Palatinate, Alsace-Lorraine, Hartz mountains.

III. Germany (new) Nordmark, Mecklenberg, Hannover, Mittelelbe-Hartz, Mark Brandenburg, Pommern; (old) Schleswig-Holstein, Mecklenburg, Pommerania, Brandenburg, Hannover, Oldenburg, Lippe; Denmark.

IV. Germany: (new) Grenzmark, Schlesien, Silesia, Östpreussen; (old) East and West Prussia, Posen, Silesia.

P. (New) Poland, Moravia, Bulgaria, Jugoslavia, Östmark, Hungary, Czechoslovakia; (old) Austria, Bohemia, Latvia, Galicia.

R. Russia in the regions of Novgorod, Pskov, Rossieny, Mogilev, Smolensk, Moscow, Tversk, Volinsk, Nizhni-Novgorod (=Gorky), Kazan, Riazan, Tula, Vladimirsk, Kiev, Chernigov, Ostrov, Kursk, Ural provinces, White Russia, Kaluga.

(c) *Fluctuations in different districts*

The full data for the outbreaks of insects and other injurious invertebrates are too voluminous to be presented in this publication. They have therefore been deposited for reference at Oxford and at Norman, Oklahoma (see References). The graphed data for the areas described above are presented in Fig. 3. As explained in a previous section, all records and references to an outbreak of a given species are taken as pertaining to the same outbreak and are considered as confirmatory, and not as supplementary records. The graph is a portrayal of the number of species which were undergoing outbreak each year in each district. For convenience in comparing the fluctuations in outbreak frequency, data of the regions are presented in parallel graphings.

As mentioned in a previous section, there are now available the more recent government reports for England and Wales and for Poland. These present a much greater amount of data for their respective areas than had been available previous to their publication. Because of their comparative completeness, they are not altogether comparable to the available records for the preceding periods. The data for the two countries, therefore, were considered separately and are discussed in the following two sections.

The Polish Government Report. The data are difficult to use because of the marked discrepancy in the numbers of reports of outbreaks each year. When, however, the number of species reported each year is considered, a fluctuation trend becomes apparent as is shown in Fig. 4; the peak years are 1921?, 1924, 1926? and 1930.

England and Wales. The data for England and Wales, as published in the Ministry of Agriculture and Fisheries reports were also considered separately from the casual reports which appeared in the literature. Frequent indications were given in the reports as to the status of insect abundance for the more injurious insects: whether or not there were more, less, or equal to average

abundance; the totals for each year as reported are indicated in Fig. 5, line 1 being the one which concerns us here. "2" indicates species which were important in their devastations, but were not reported as being at their maxima. "3" indicates those species which were not included in the 1928 list of usually injurious insects, and "4", those species which were reported as being in a stage of "decreasing" injuriousness from their usual abundance. The peaks here are those for 1921, 1925?, 1928 and 1933.

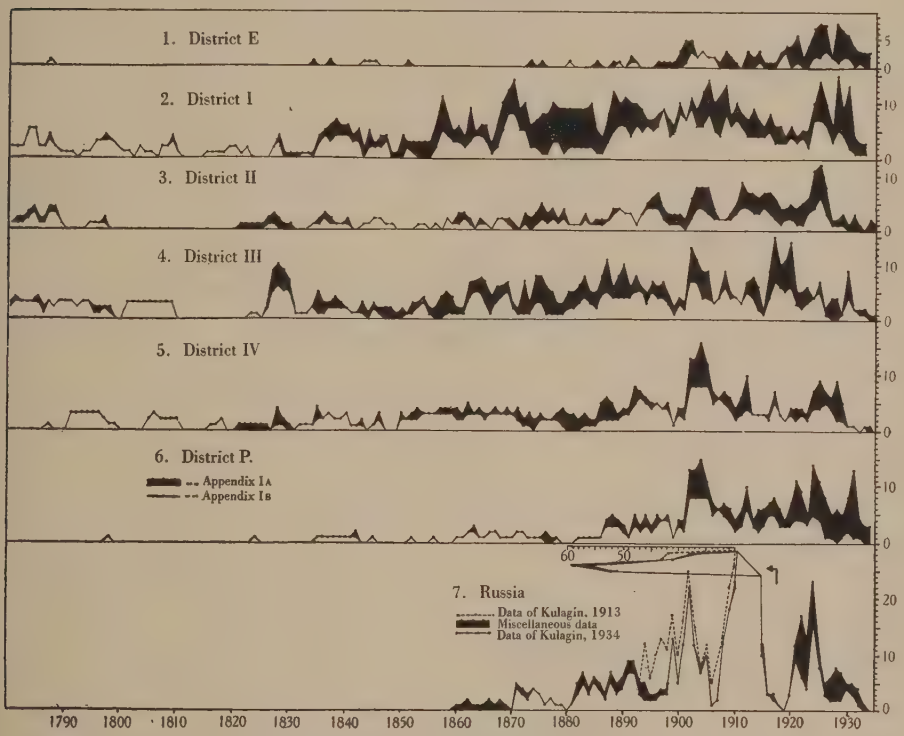

Fig. 3. Fluctuations in the numbers of insect outbreaks in the deciduous forest area of Europe, considered by districts (see Fig. 2). Yearly totals for the entire area shown in Fig. 6.

For an examination of the data presented by Kulagin (1913), see p. 128 where they are compared with the other biotic areas of Russia.

(*d*) *Fluctuations in the area as a whole*

A graph depicting the sum of the massed data for all of the individual subareas within the deciduous forest area is presented in Fig. 6. In effect this graph is the result obtained when the data for the individual subareas of the

deciduous forest area were added together: thus it embodies the realization that an outbreak spread over a great area has more individuals present than one restricted to a smaller region (and hence in but one subarea). This differs from the method of constructing the graphs of Fig. 3 where several records of outbreak for one species in a single subarea were considered as pertaining to the same outbreak. Thus, strictly speaking, Fig. 6 is more of an indication of changes in population density than of the number of individual species

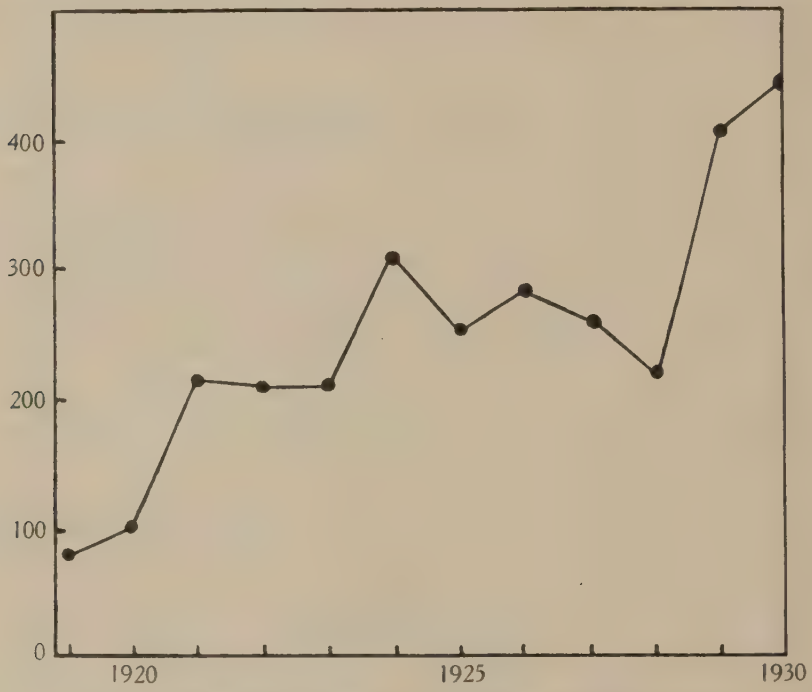

Fig. 4. Fluctuations in the numbers of insect outbreaks in Poland, 1919–30. (Data from Ruszkowski.)

which underwent outbreak in any given year; but for convenience these peaks will be designated in terms of "peak years of outbreak abundance".

In analysing the general outbreak frequency curve for species which had the same rhythm as the biota as a whole several things became evident. Nearly all of the species for which there were copious records showed a condition of what may be termed "prolonged outbreak", i.e. they were reported as being injurious for several years continuously, a property which distinguished them from the others which usually had, at most, two consecutive years of outbreak in any area. Thus it became necessary to consider these two groups separately with reference to their behaviour in the general fluctuations.

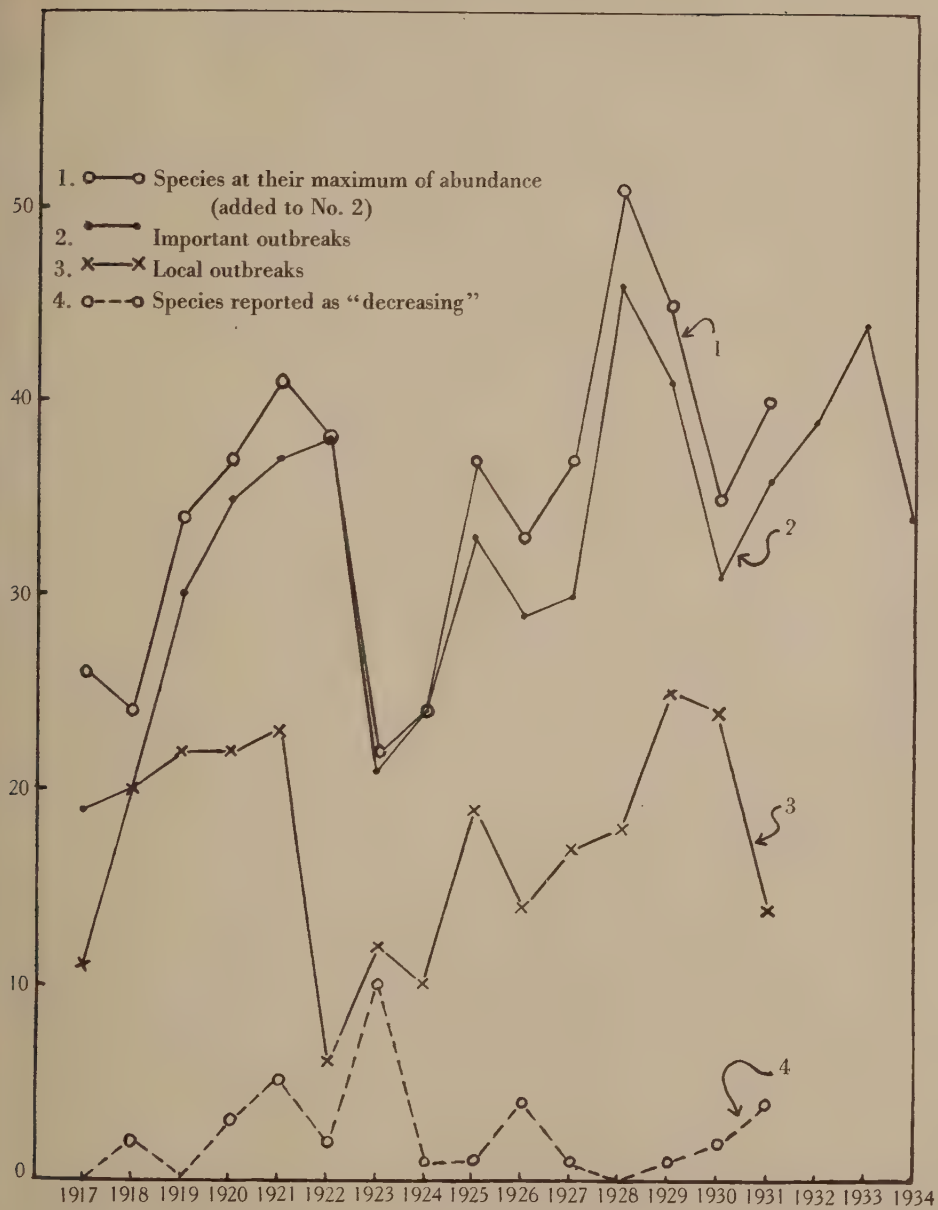

Fig. 5. Fluctuations in the numbers of insect outbreaks in England and Wales, 1917–34.

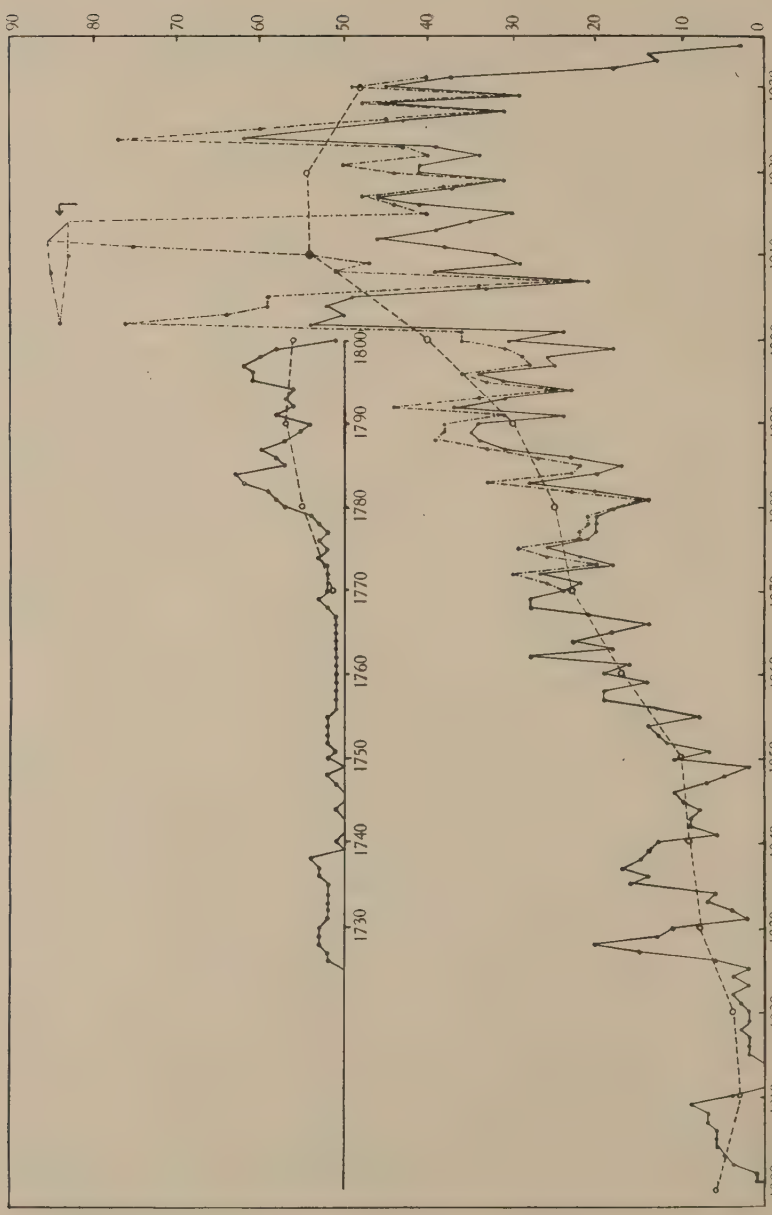

Fig. 6. Fluctuations in the numbers of outbreaks in the deciduous forest area. Being a summary of the data in Fig. 3. (Government reports, Figs. 4 and 5, not included.)

—•—•— Usual data. —•—•— Data of Kulagin, 1934 (U.S.S.R.). (For totals, read top line.)

—— ○ —— Trend line: obtained by plotting means for 20-year periods.

The data for the abundant records group—16 species[1]—were examined, note being made of the conditions of the population at the time of the general fluctuation peaks. These conditions were classified under the following ten types:

A. Peak of abundance reached during
B. A new prolonged outbreak beginning at
C. Increased abundance starting with
D. New prolonged outbreak beginning shortly after
E. New prolonged outbreak beginning shortly before
F. Subsidence of outbreak during
G. Decrease in abundance during
H. Subsidence of prolonged outbreak shortly before
I. Subsidence of prolonged outbreak shortly after

} the year of peak in the general fluctuation

— Outbreak continued at normal intensity with no reference to general fluctuation
No record; impossible to evaluate because there is no assurance that the data are complete

The data summarizing this analysis are given on p. 122 (Table 1). It appears that the peak year of the general cycle *is* reflected in the behaviour of these species for (omitting "no record" years, because there is no assurance that there was no outbreak for that year) out of 204 cases, only 32 show no effects of the year. Peaks are noted in 20 (10·4 %) cases. increases in 72 (35·1 %) giving a total of 92 (45·0 %) cases of increase (or 53·5 % of the cases of some population change, i.e. omitting the 32 cases of "no change"). Decreases associated with the year, on the other hand, exhibit 80 examples (39·2 %). There thus appears to be some sort of general change in population trends on the occasions of large insect populations, the nature of which is not clear. This trend exhibits an alternation of general increases and decreases which is seen on examination of the last two columns of Table 1.

Certain other species whose outbreaks were more or less confined to a single year in any given area were found to be much more characteristic of the general outbreak cycle than were others. It appears that the following species are fairly closely associated in their periods of outbreak with the general trend.

Area E. *Plutella maculipennis, Chlorops taenopus, Hyponomeuta malinella* (?). "Tipulidae".

Area I. *Agrolimax terrestris, Cephalea* spp., *Chloropisca* spp., *Coleophora laricella, Myelophilus* spp., *Nematus abietinus, Strophosomus* spp.

Area II. *Agrolimax terrestris, Chloropisca* spp., *Dendrolimus micans, Strophosomus* spp.

Area III. *Cecidomyia destructor, Cephalea* spp., *Cheimatobia boreata, Chlorops taenopus, Cnethocampa* spp., *Hylobius abietus, Otiorrhynchus* spp., *Pissodes* spp., *Strophosomus* spp., Tipulidae.

Area IV. *Chlorops taenopus, Cnethocampa* spp., Tipulidae.

Area P. *Hylemyia coarctata, Hylobius abietus.*

Area R. *Aporia crataegi, Loxostege destructor, Phyllotreta nemorum, Pieris brassicae.*

[1] *Bupalus pinarius, Cheimatobia brumata, Chlorops taenopus* Mg. (=*pumilionis* Bjerk.), *Cicadula* (*Jassus*) 6-*notata, Dasychira pudibunda, Dendrolimus pini, Diprion* (*Lophyrus*) *pini, D.* (*L.*) *sertifer* Geoff. (=*rufus* Pz.), *Grapholitha tedella, Ips curvidens, I. typographus* L., *Panolis flammea* Schiff. (=*piniperda* Esp.; "*Noctua griseovariegata* Goez."), *Pegomyia hyosciami, Porthetria* (*Lymantria, Liparis*) *dispar, P. monacha, Tortrix viridana.*

Table 1. *The reaction of certain abundant species to years of great general insect abundance*

For an explanation of the letters A–I, see text. The small letters at the heads of the columns refer to species as follows: *k* = *Bupalus pinarius*, *l* = *Cicadula 6-notata*, *m* = *Dasychira pudibunda*, *n* = *Cheimatobia brumata*, *o* = *Dendrolimus pini*, *p* = *Diprion (L.) pini*, *q* = *Grapholitha tedella*, *r* = *Ips curvidens*, *s* = *Ips typographus*, *t* = *Diprion (L.) sertifer*, *u* = *Panolis flammea*, *v* = *Porthetria dispar*, *w* = *Porthetria monacha*, *x* = "Raupenfrass", *y* = *Tortrix viridana*, *z* = *Pegomyia hyosciami*; "+" = total instances of population increase, "–" = total instances of population decrease.

	k	*l*	*m*	*n*	*o*	*p*	*q*	*r*	*s*	*t*	*u*	*v*	*w*	*x*	*y*	*z*	A	B	C	D	E	F	G	H	I	—	+	–
1931?	.	.	H	.	–	H	.	.	.	.	–	.	A	.	.	.	1	.	.	.	.	.	.	2	.	2	.	2
1928	–	.	.	.	–	B	A	.	A	F	D	.	H	.	.	.	2	1	.	1	.	1	.	1	.	2	2	2
1924	B	B	.	.	B	.	.	.	F	.	–	A	F	.	B	C	1	4	1	.	.	2	.	.	.	1	5	2
1921?	.	B	.	.	D	.	.	.	C	G	D	.	C	.	F	C	.	1	3	2	.	1	1	.	.	.	6	2
1917?	C	F	A	G	–	F	.	.	G	.	–	F	C	..	–	–	1	.	2	.	.	3	2	.	.	4	2	5
1913	G	G	.	B	E	.	.	.	H	F	G	.	H	.	F	C	.	1	1	.	1	2	3	2	.	.	3	7
1908?	G	–	.	.	G	G	.	.	–	–	B	–	C	.	G	A	1	1	1	.	.	.	4	.	.	4	2	4
1902	C	G	F	D	FB	B	.	B	B	D	G	B	G	.	B	D	.	6	1	3	.	2	3	.	.	.	10	5
1896?	–	I	.	F	F	–	D	A	.	.	G	I	–	.	F	.	1	.	.	1	.	3	1	.	2	3	1	6
1892	C	D	B	B	G	C	A	.	–	.	–	–	B	.	G	B	1	4	2	1	.	.	2	.	.	3	7	2
1888?	C	.	F	H	–	D	.	.	I	.	C	B	C	.	B	.	.	2	3	1	.	1	.	1	1	1	6	3
1883	F	.	.	F	C	.	.	A	E	.	A	.	.	.	D	.	2	.	1	1	1	2	.	.	.	.	3	2
1875	F	.	.	.	B	.	.	.	G	.	H	F	C	.	A	.	1	1	1	.	.	2	1	1	.	.	2	4
1872	G	.	.	F	F	B	.	H	C	.	A	.	C	.	F	.	1	1	2	.	.	3	1	1	.	.	3	5
1869	.	.	.	B	–	.	B	B	–	.	F	.	–	.	FB	.	.	4	.	.	.	2	.	.	.	3	4	2
1863	I	.	.	.	D	.	B	.	–	.	B	.	.	.	H	.	.	2	.	1	.	.	.	1	1	1	3	2
1854	.	.	H	.	C	.	B	.	B	.	H	F	A	.	F	.	1	2	1	.	.	2	.	2	.	.	3	4
1846	.	.	D	.	G	.	B	.	F	.	G	.	A	.	F	.	1	1	.	1	.	2	2	.	.	.	2	4
1837	D	.	.	.	–	.	.	.	–	.	A	.	C	.	A	.	2	.	1	1	.	.	.	.	.	2	2	.
1828	–	.	.	.	F	E	.	.	A	.	FB	–	C	.	–	.	1	1	1	.	1	2	.	.	.	3	1	1
1818?	.	.	.	.	.	D	.	.	A	.	–	.	F	.	.	.	1	.	.	1	.	1	.	.	.	1	.	4
1809	.	.	.	.	F	.	.	.	H	.	G	.	G	.	.	.	.	.	.	.	.	1	2	1	.	.	2	4
1797	F	.	.	.	H	.	.	.	–	.	H	.	F	B	D	.	.	1	.	1	.	2	.	2	.	1	.	5
1784	F	.	.	.	G	–	.	A	G	.	F	.	.	G	.	.	1	.	.	.	.	2	3	.	.	1	1	.
1769	.	.	.	.	.	.	.	.	B	.	.	.	.	–	.	.	.	1	.	.	.	.	.	.	.	1	1	.
1755	.	.	.	.	F	.	.	.	.	.	.	.	.	–	.	.	.	.	.	.	.	1	.	.	.	1	.	1
1744	.	.	.	.	.	.	.	.	.	.	.	.	.	.	A	.	1	.	.	.	.	.	.	.	.	.	.	.

Total																		
A	.	.	1	.	.	.	2	3	3	.	3	1	3	.	3	1
B	1	2	1	3	3	3	4	2	3	.	3	2	1	1	4	1
C	4	.	.	.	2	1	.	.	2	.	1	.	8	.	.	3
D	1	1	1	1	2	2	1	.	.	1	2	.	.	.	2	1
E	.	.	.	.	1	1	.	.	1	.	.	.	.	.	.	.
F	4	1	2	3	6	1	.	.	2	2	3	3	3	.	7	.
G	3	2	.	1	4	1	.	.	3	1	5	.	2	1	2	.
H	.	.	2	1	1	1	.	1	2	.	3	.	2	.	1	.
I	1	1	.	.	.	.	.	.	1	.	.	1	.	.	.	.
—	3	1	.	.	6	2	.	.	6	1	5	3	2	2	2	1

These may be considered as the characteristic species of the times of greatest outbreak abundance. Few of the species are duplicated in different areas in the above list. This would seem to show that the peaks of outbreak frequency are not altogether caused, as might possibly be expected, by the influence of recurring abundance of records of one or two species. Apparently a number of factors are at work, and one is led to the opinion that the question of biotic balance is an important item in this connexion.

After 1850 we find that there was an increase in the recording of insect outbreaks, and new species begin appearing shortly after that time. To see exactly how representative the data for the pre-1850 period were for the insect population as a whole, there have only to be considered separately the

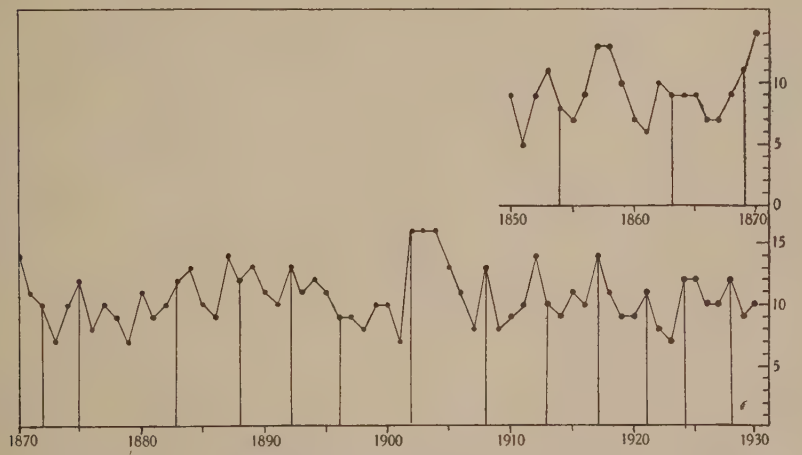

Fig. 7. Fluctuations in the species recorded before 1850 with peaks in the general trend since 1850 indicated by vertical lines.

species which were recorded before 1850. This has been done, and the results of this separate consideration are shown in the accompanying graph (Fig. 7) in comparison with the peaks found when using all available data. We find that there is a rather close correlation between the two sets of peaks: 8 peaks coincide exactly; 6 are within one year of occurring together (3 occurring one year before, and 3 one year after), while there is one pre-1850 species peak which has no all-species counterpart, and two all-species peaks which have none in the pre-1850-species data. In other words, 50 % of the peaks concerned coincide, and 82·4 % of them coincide to within one year (i.e. peak year $\pm$ 1). This give a rough index of the reliability of the pre-1850 data as compared with the more recent records.

The species concerned in this category are those having several (three or more) outbreaks before 1850; they are: *Porthetria dispar, Bupalus pinarius*

Diprion pini, *Ips typographus*, *Dendrolimus pini*, *Porthetria monacha*, *Panolis flammea*, *Tortrix viridana*, "*Noctua griseovariegata*" (=*Panolis flammea*), *Cnethocampa pinivora*, *Dasychira pudibunda*, *Enarmonia diniana*, *Euxoa segetum*, *Grapholitha tedella*, *Hylastes cuniculatus*, *Ips curvidens*, *Malacasoma neustria*, *Nematus abietinus* and *laricis*, *Otiorrhynchus niger*, *Phytometra gamma*, *Polychrosis botrana*, *Sirex juvencus* and sp., *Strophosomus obesus*, *Tenthredo pini*, and *Tortrix bouliana* and *resinella*. Important in the pre-1850 records, but not occurring after 1850 (at least, not under that name) were "Raupenfrass" and "Borkenkäfer".

In examining the summarized data of the deciduous forest area as a whole let us examine the dates when most outbreaks occurred, when all the data are massed together (see Table 2 which is a summary of these peaks). These peaks

Table 2. *Correlation between the years of outbreak in sections of the European deciduous forest area.* (*Dubious peaks are indicated by a query*)

Entire area	Pre-1850 spp.	England	E	I	II	III	IV	P	Poland	R
—	—	1932–3	—	—	—	—	—	—	—	—
1931?	—	—	—	1930	1931?	1930	1931	1931	—	1931
—	—	1929	—	—	1929?	—	—	—	1929–30	—
1928?	1928	1928	1928	1928	—	—	1928	—	—	1928
1924	1924–5	1925	1925–6	1925	1925	1925	1925	—	—	—
1921?	1921	1921	1921	1920?	—	1920	1920–2?	1921	1921?	1922
1917?	1917	—	—	—	—	1917	1917	1917	—	—
—	—	—	—	1916?	1915–16	—	—	—	—	—
1913	1912	—	1914?	1913	.....	1913	—	—	—	1913
—	—	—	1912?	—	1911...	—	1912	1912	—	—
—	—	—	—	1910?	—	—	—	—	—	1910?
1908?	1908	—	1908	1908	—	1908	1908?	1908?	—	1907
—	—	—	1904?	1905	1905	—	1904	1904	—	1905
1902	1902–4	—	1901–2	—	1903...	1902	1902...	1902...	—	1902
—	—	—	—	1900	—	—	—	—	—	1899
—	—	—	—	—	—	1897?	1898?	1898	—	1897
1896?	—	—	—	—	1896	1895?	—	—	—	—
—	—	—	—	—	—	—	—	—	—	1894
1892	1892	—	1891?	—	—	1892?	1892	1892	—	—
1888?	1886	—	—	1888	1888–9	1887	1887	1888	—	1888
—	—	—	—	—	—	—	—	—	—	1885?
1883	1883	—	—	1884	1883?	1883	—	—	—	1883
—	—	—	—	.....	—	—	1879	—	—	—
1877	1875	—	—	1877...	1875	1874–5	—	1876?	—	1874
1872?	1870	—	—	1872?	—	1872?	—	1871–2?	—	1871
1869	—	—	—	1870	1867–9?	1869?	—	1866–7	—	1866
1863	1862	—	—	1862	1860–1	1864?	—	1863	—	1862?
—	1857–8	—	—	1857	—	1858	—	—	—	—
1854	1853	—	—	—	1854	—	1854?	1854?	—	—
—	1846	—	—	1846–7	1845–6	1845?	1846	—	—	—
—	—	—	—	1844?	—	1843?	—	1842?	—	—
—	1837	—	—	1838?	—	1838?	'37? '39?	1839?	—	—
—	—	—	—	—	1836	1835?	1835?	—	—	—
—	1828	—	—	1828	1827	1828	1828	1824?	—	—
—	1818?	—	—	1819–20	—	—	1818?	—	—	—
—	1809	—	—	1809	—	1809	—	—	—	
—	—	—	—	1803?	—	1802	1806?	—	—	
—	1797	—	—	1797	1799?	1790–5	1791–6	1798??	—	—
—		—	—	1787?	1787–9	1786	—	—	—	—
—	1784	—	—	1783–4	1784	1782	—	—	—	—
—	1769	—	—	—	—	—	—	—	—	—
—	1755	—	—	—	—	—	—	—	—	—
—	1744	—	—	—	—	—	—	—	—	—

have what at first may be thought to be irregular intervals between them and at times it is difficult to decide what constitutes a true peak. However, when these intervals are plotted against the time sequence (see Fig. 8) it will be seen that there has been a gradual regression in the length of time between the years when outbreaks were particularly numerous. In this latter graph the intervals between the "dubious" peaks (i.e. those marked by queries) have been plotted by "●", between the more definite peaks by "o", and the intervals between the definite peaks, ignoring any intervening dubious peaks, by "ϕ". When the symbols "o" and "ϕ" are considered as representing the

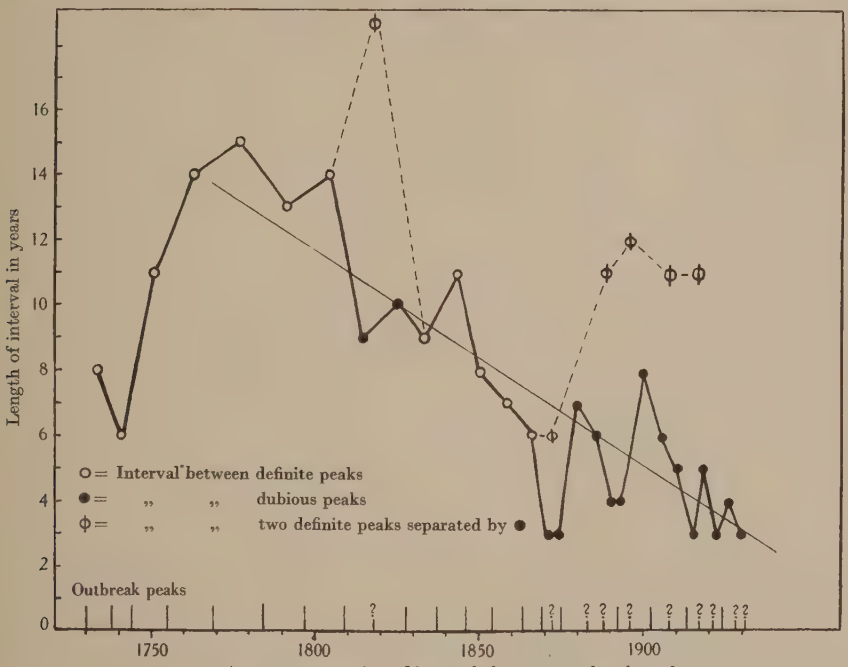

Fig. 8. Apparent regression of intervals between outbreak peaks.

true condition, much of the regression trend disappears, and a type of cycle appears. From the nature of the data it is not possible to indicate which is the correct analysis. The average interval between all peaks is 7·4 years, that between the more distinct peaks (i.e. o and ϕ), 10·7 years.

4. Biotic areas other than the deciduous forest

(*a*) *Subdivisions*

(1) The *Tundra* is composed of the regions north of about the 10° C. isotherm: the limit of tree growth. Here are found long cold winters and very short summers; there is low precipitation. Vegetation is restricted to mosses,

a few grasses, many grey lichens and a few dwarf bushes and creeping undergrowth. It has been for the most part, until very recently, agriculturally undeveloped and no insect outbreaks have been noticed.

(2) The *Transcontinental Coniferous Forest* or *Taiga* is, as its name implies, a transcontinental belt of forest, mostly conifers, which is characteristic of high boreal latitudes. The dominant trees are the spruce and pine, with birch and aspen in the subclimax areas. The composition is, for the most part, unchanged throughout its entire extent, except that the larch is added in northern European Russia. The chief crops here are oats, barley, potatoes, and timber. A few cattle meadows are present in cleared areas, but for the most part the entire zone is still forested. The soil is very moist and podzolic, and much of it is undrained, except in hilly areas.

(3) *Deciduous Forest-steppe.* The Russian Deciduous Forest area is largely unglaciated and non-mountainous. There is a liberal admixture of conifers in the north, and a great area of intergradation into the steppe or prairie area in the south. So wide is this "forest-steppe" area of ecotone that it was found necessary to consider it as a separate zone in the consideration of the outbreaks here. This parkland aspect is similar to that of its North American equivalent (e.g. in Illinois) and is present for largely the same reasons: soil differences along an ecotone resulting in local moisture deficiency.

(4) The *Steppe*, like the coniferous forest, is a belt stretching nearly across the Eurasian plains. It has a semi-arid continental climate with short hot summers with limited rainfall, and long cold winters. To-day the European steppe is largely ploughed, and is characterized by cereal culture (wheat, rye, barley, oats), potatoes, sunflowers, cabbages, and in the south by cotton and vines as well. A wide forest-steppe zone is conspicuous on the northern border: it is probably the most fertile portion of the steppe, containing the famous "central black soil [chernozem] area". Much of the southern steppe is too sandy or marshy to permit good cultivation and has been a breeding place in the past for migratory locusts. The principal pests are (1) those usually common in converted grassland: grasshoppers, cutworms, and white grubs, (2) cereal pests, and (3) pests of cotton, vine and market-garden crops. There are few forest pests in the steppe proper. Formerly Russian agricultural method involved letting fields "lie fallow" for several years as a part of the crop rotation system, these fallow places frequently serving as breeding areas for injurious locusts and grasshoppers. This practice has largely been abandoned under the present Soviet administration.

(5) The Russian grass steppe dwindles into a salt *Semi-desert* in the regions about the Caspian Sea. Here the vegetation is abundant only locally, and consists largely of wormwood (*Artemisia*) scrub, with much barren ground. There is little agricultural tilling done here.

(6) The *Caucasian Forest Area* is characterized by its diversity of vegetation zones. The steppe approaches the Caucasus mountains from the north and

gives way to a band of deciduous trees, largely oak. Above are conifers and mountain meadows. Forestry and grazing are the chief agricultural pursuits.

(*b*) *Insect outbreaks*

Much less data are available for these biotic areas than were found for the adjacent deciduous forest area. However, the same method was used in the

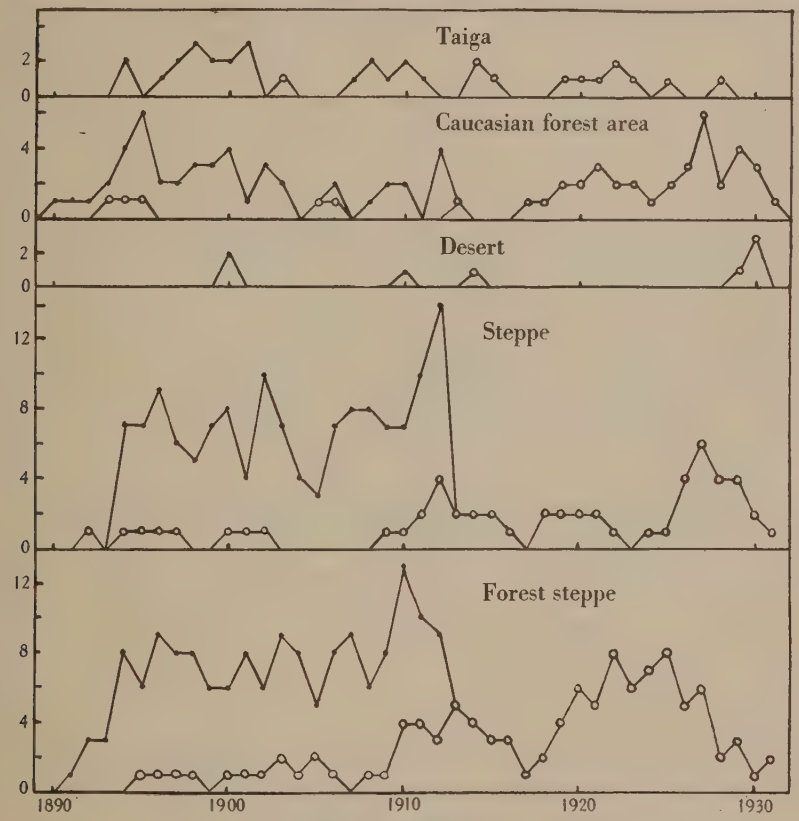

Fig. 9. Russian data.

—•—•— Data from Kulagin, 1913. —○—○ Usual data.

processing of the data as was used for those of the forest area. The shorter length of time for which data are available, together with an accompanying scarcity of data during this time, enables one to draw fewer conclusions regarding the nature of the fluctuations here.

Fig. 9 shows some peaks which are readily evident, and a number which are much less evident, largely due to scarcity of data. The more conspicuous of the latter peaks may be provisionally accepted for the sake of comparisons,

with reservations indicated by a query. A comparative chart of these peaks, together with those of the deciduous forest, is presented in Table 5. There is a slight tendency for outbreaks in the drier areas (i.e. semi-desert and steppe) to precede those in the more moist forested areas; also, that while there is some evidence that major currents of outbreaks are present throughout all areas at certain times (e.g. 1883–4, 1900–2, 1907–8, 1927–8), it is contended that there is less correspondence shown between the different biotic areas than between the subareas of the deciduous forest. There is also a tendency, less well expressed, for areas having more or less similar climates to have peaks the same year, e.g. the moist areas in 1883–4 and 1894, the drier-than-forest areas in 1927 and 1910, and the southern areas in 1900.

(c) *The Russian data of Kulagin*

As has been mentioned, one of the difficulties in studying the problem of outbreaks as it is attacked in this study is the comparing and consolidating of the data obtained by various workers under different conditions and with different criteria for an outbreak. The 1913 study of Kulagin presents data from 48 principal stations in European Russia ranging from the taiga to the semi-desert and Caucasian forests, giving an opportunity to compare fluctuations in different ecological community areas with records collected by one man with a given standard of selection.

Two methods of analysing these data were used: one, the usual, counting all citations of a species outbreak in an area as pertaining to the same outbreak; and the second, using the number of citations as an index of intensity, a method which was found to be unsatisfactory for ordinary data. The results under the two methods are tabulated in Table 3 and are graphed in Fig. 10.

Table 3. *Synopsis of the data presented by Kulagin*, 1933

Biotic area ...	93	94	95	96	97	98	99	00	01	02	03	04	05	06	07	08	09	10	11	12
A																				
Taiga	.	2	.	1	2	4	2	2	3	.	.	.	1	.	1	3	2	1	1	.
Deciduous forest	2	23	10	12	23	19	9	9	11	5	8	7	2	8	11	12	8	10	9	12
Forest-steppe	.	19	20	24	17	20	14	11	16	13	21	7	14	17	17	16	11	23	16	20
Steppe	.	10	13	19	16	13	11	12	8	4	13	6	4	10	13	15	10	13	15	21
Semi-desert	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.
Caucasian forest	.	3	5	2	2	3	3	4	1	3	2	.	.	1	.	1	2	2	.	4
B																				
Taiga	.	2	.	1	2	3	2	2	3	.	.	.	.	.	1	2	1	2	1	.
Deciduous forest	2	7	3	7	9	7	4	5	4	3	3	2	2	4	4	3	5	4	6	5
Forest-steppe	.	7	8	9	5	5	6	4	6	5	9	3	5	5	5	7	6	7	7	10
Steppe	.	6	6	8	5	5	8	8	3	9	7	4	3	7	8	8	6	6	8	10
Semi-desert	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	1	.	.
Caucasian forest	.	3	5	2	2	3	3	4	1	3	2	.	.	1	.	1	2	2	.	4

The principal stations listed by Kulagin (indicated by * in the list on p. 113) were reported as having outbreaks of the following species: 1, *Eurygaster maura* Fabr., *maroccana* Fabr., and *integriceps* Osch.; 2, *Agriotes segetis* Bjerk. and *Atheus niger* L.; 3, "Thrips"; 4, *Cecidomyia destructor* Say; 5, *Lema melanopla* L.; 6, *Hydroecia nictitans* Bkh.; 7, *Oscinus frit* L.; 8, *Anisoplia austrica* Hbst.; 9, *Agrotus segetum* Schiff.; 10, *Cephus pygmaeus* L. and *tabidus* Fabr.; 11, *Tapinostola musculosa* Hbst.; and 12, (*Calliptamus italicus*, *Locusta migratoria*, and "grasshoppers"). The first method outlined in the text was used in preparing the "B" portion of the table, and the second method the "A" portion.

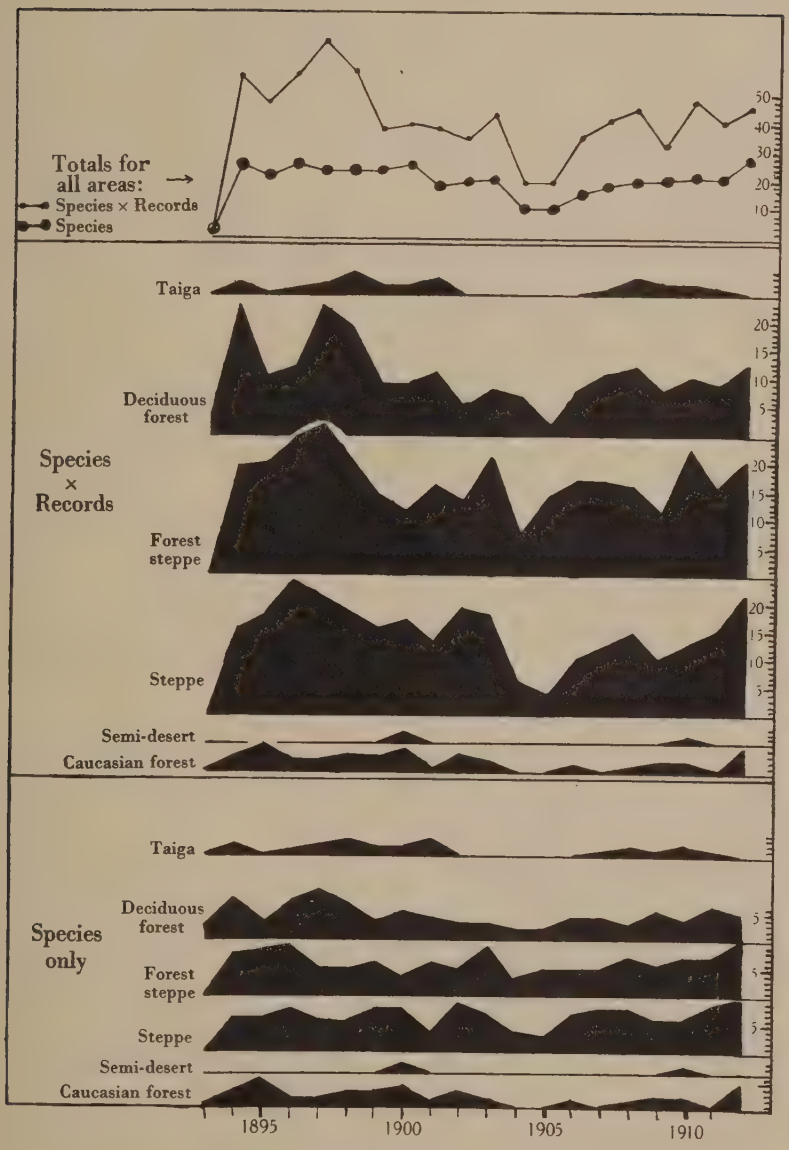

Fig. 10. Russian data of Kulagin, 1913.

5. Periodic insects and their fluctuations in numbers

(*a*) *Cockchafer* (Melolontha) *fluctuations*

An insect which has been much reported in the literature as undergoing "outbreaks" is the cockchafter (Maikäfer, Hanneton), *Melolontha*. It occupies a position apart from the majority of other insects, in taking more than one or two years for its life cycle and presenting the phenomenon of "broods": a situation in which several years are taken for the completion of the life history, the group of individuals beginning and completing the cycle synchronously and emerging the same year being termed a brood. It frequently happens that of the theoretically possible number of broods of a species, one brood appears in a particular locality with an abundance of individuals, while the other broods may have a much smaller number of individuals or may not be known at all (see Prell, 1929, 1930). A similar phenomenon is found in the 13- and 17-year "periodical cicada" (17-year "locust": *Cicada septemdecim*) and "white grubs" or May beetles ("June bugs": *Phyllophaga* spp.) in North America.

The item of prolonged metamorphosis has interested a number of workers, but the regional distribution of the different broods brings in still more fascinating problems. *Melolontha* has two important species found in Europe: *melolontha*, which has a 3–4-year life cycle, and *hippocastani*, which usually has a 4–5-year cycle. The generalization usually made regarding the length of time for metamorphosis is that there is a 3-year period north of the Main, a 4-year period in North Germany, and a 5-year period in north-eastern Prussia and the Scandinavian countries.

Inasmuch as *Melolontha* has a regular 3–4–5-year regional cycle, it is obvious that the numerous reports of its "outbreaks" which appear in the literature must be discounted as they refer to the normal appearances of the adult insects.[1] It is here that the desirability of having more exact data as to insect abundance in addition to the mere "presence-absence" accounts becomes most noticeable.

The only data which we have regarding actual numbers are those published by Decoppet (1920) for districts near Zürich in Switzerland, these being obtained from data relating to the compulsory collections of the adult beetles by local ordinance. Two broods of the insect *Melolontha* are present in this region, the Uranian (1901 4) and the Bernian (1900-3) flight year broods. The former brood had its peak years of abundance in 1844?, 1850, 1871, 1892, 1904? and 1901; the latter in 1807, 1827,[2] 1879, 1903, 1909 and 1918. It will

[1] A good list of such references may be found in Prell, 1929. Rethley (1925) lists for Hungary 1616, 1684 and 1824 which may or may not have been particularly severe years of abundance, Rudy (1926) mentions 1479 and 1827 for Switzerland.

[2] Data from Rudy (1926).

be seen that there is a slight tendency for peaks to occur in somewhat less than 20-year periods in the Uranian brood and in 20–25-year periods in the Bernian, although the data are insufficient to warrant definite conclusions being made.

(*b*) *Invasions of migratory locusts*

The migratory locusts which have periodically invaded Europe and other areas cannot be considered as representing a part of the native insect population since the factors which regulate their abundance are not those which govern the insect populations of the areas invaded. While the general problem of locust outbreaks in the breeding areas may be found discussed in many recent textbooks of entomology, certain aspects of the problem may be mentioned here. (A good summary of the subject may be found in Imms (1937).) Our knowledge of the cause of the changes in the recent nature of locust outbreaks as far as Central Europe is concerned is unsatisfactory. The locusts which swept over Europe in previous centuries have, apparently, greatly decreased. It is the opinion of Filipev (1929) that the areas which supported the principal breeding grounds for *Locusta migratoria rossica* were in the steppes of Hungary and Ukraine, and that there were secondary breeding grounds farther west where mass breeding occurred only in exceptionally dry and hot years. While the argument has been raised that, in destroying the breeding grounds suitable for *Locusta*, others were created for *Dociostaurus maroccanus*, there certainly have been fewer large-scale invasions into middle and western Europe in recent years. This would be one reason for considering that most (if not all) of the middle western European locust visitations of the past pertained to *Locusta* if other evidences were lacking. It is interesting to note that in these invasions it is usual for certain routes to be followed: *Locusta migratoria* usually migrated west and north via the upper Danube and the Main valleys into the Rhine and Valais regions, from at least its southern breeding places in Hungary, Ukraine and areas near the Black Sea. Zolk (1934) presents an interesting map of other routes which are taken, from the north-west Black Sea grounds to north Germany via Poland and Silesia to Hamburg and the lower Rhine and from the east Black Sea, Caspian and eastern lake areas north-west across Moscow to Leningrad, Esthonia and Finland. The north Russian breeding places (in the Kazan-Samara and Ryazan areas) probably contributed to the invasions to some extent and certainly refer to the "outbreaks" reported for the Moscow area. A map of the breeding areas of the Russian locusts may be found in the papers of Filipev (1929) and of Zolk (1934).

The details of the habitat conditions of the breeding areas of the locusts are decidedly an ecological problem. It should be noted that while *Locusta migratoria* breeds in the south of Russia in swampy areas and in the north in disturbed sandy habitats, its main migration trend is towards the deciduous

forest area. *Dociostaurus maroccanus* breeds in the low stony mountains and migrates into the hot dry plains of the Crimea, the Caucasian region and Turkestan, breeding secondarily in the new areas. *Schistocerca gregaria* has, at various observed times, begun its migration in the upper Niger regions, migrating into the Sudan, and thence into South Africa, skirting the moist tropical districts and restricting itself to steppe areas. From Rhodesia southwards it mingles with swarms of *Nomadacris septemfasciata*.

The reason for this directional movement in these different cases can only be speculated upon, but the effects of their activity on the biota of the regions invaded is obvious. Here is a change in microclimate in one area greatly influencing the biotic balance of regions a thousand miles distant. The effect on the human food supply is well known; that on animal food can only be conjectured. This is a sporadic factor of the same general category as the migrations of the lemming (*Lemmus*), nutcracker (*Caryocatactes*) and short-eared owl (*Asio flammeus*) migrations, which has profound biotic effects on any area visited. The fact that these invasions have been considered periodic or to be correlated with sunspots has been mentioned in the first section. The present section will consider the reports of outbreaks which probably pertain to *Locusta migratoria*, the locust which has usually been responsible for the invasions of the deciduous forest area.

No chronological table of these invasions has been included, since any such account would be, for the most part, a duplication of several previous works and may be found in the references of Keppen (1870), Rudy (1923), and the U.S. Ent. Comm. Report, Vol. 2, although it must be admitted that none of these is complete in itself. A chart tabulating the recorded invasions into temperate Eurasia is included in Fig. 11. The data are summarized in terms of 5- and 10-year periods by countries, in an attempt to show certain major trends which are not so apparent when yearly periods are used.

Certain trends are at once evident: invasions are more concentrated at certain periods than at others, although at first sight there appears to be no regularity in the spacing of these concentrations. A summary of the table is presented in the form of a block graph at the bottom of the chart, the summary being the total records (as indicated in the chart) for each 5-year period. A summary in terms of 10-year periods is also included (indicated by a line graph in which the 10-year period is the decade, i.e. 1900–10). Here these trends become more obvious. Major concentrations of invasions occurred in the middle and later nineteenth century, in the last quarter of the seventeenth and the first half of the eighteenth centuries, and so on. Within these major trends certain minor peaks occur, e.g. about 1890, 1850, 1810, etc. These minor peaks must be taken into account to afford some basis of comparison with the peaks which occur in the periods of less marked concentration much earlier. A tabulated summary of these peaks is given in Table 4.

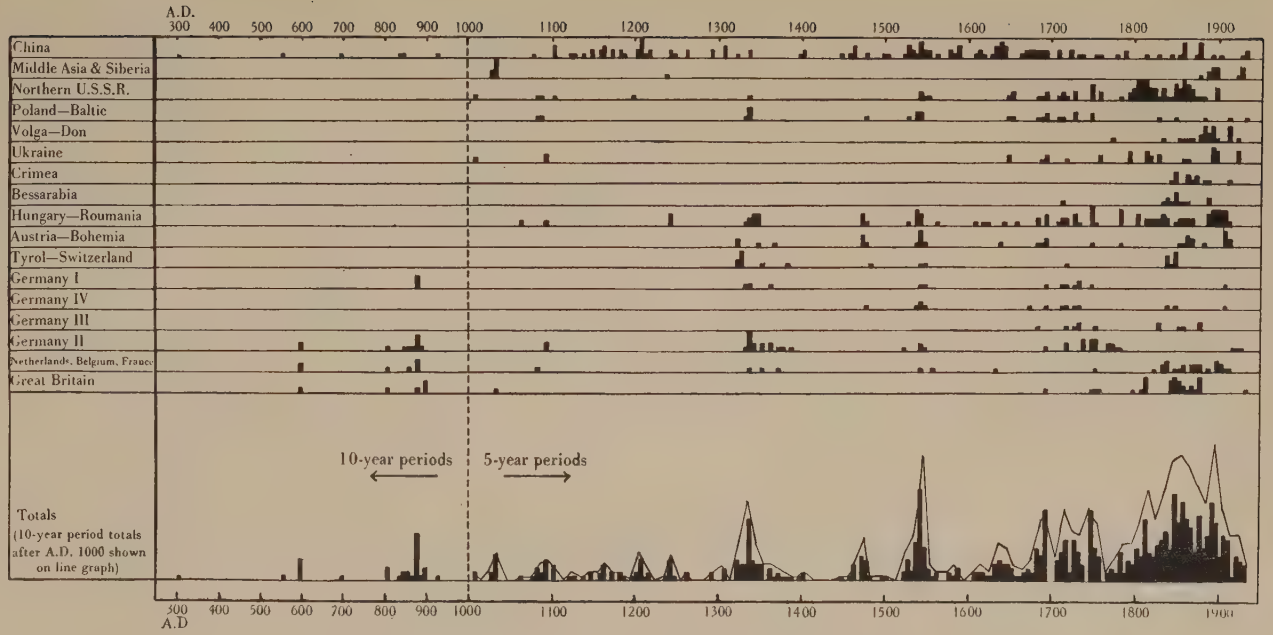

Fig. 11. Locust records in Eurasia. Shown according to political regions.

Table 4. *Peaks of abundance and their intervals for locusts* (*see Fig.* 11)

Dates indicate decades, i.e. 1905 = 1900–10. The three classes of intervals used are as follows: 1, between two peaks of undoubted existence; 2, between a peak less definitely established and any other; 3, the interval between two definite peaks when an indefinite peak intervenes.

Major concentration masses	Peaks	Intervals		
		1	2	3
1780–1880(–1915?)	1895			
	1855	40	—	—
	1815	40	—	—
	1785?	—	30	70
1680–1760	1745	—	40	—
	1715	30	—	50
	1695	20	—	—
1615–1655	1635?	60	—	—
1525–1585	1545	90	—	—
1445–1505	1475	70	—	—
	1405?	—	70	—
	1335	—	70	—
1120–1250?	1245?	—	90	—
	1205?	—	40	—
	1165?	—	40	—
	1095?	—	70	—
	935??	—	60	—
	885	—	50	—
	695	—	90	—
	595	—	100	—

6. Discussion of outbreak survey

In this study there has been an attempt at analysing the available records of insect outbreaks with the purpose of finding some indication of the insect population fluctuations of the past. The task of testing the reliability of such a study still remains to be done, since there have been no studies made on total insect populations in a given area over a large number of years. When such a study shall have been made, it will be interesting to determine the degree of correlation which appears between its fluctuations and those of the "economic" insects of the surrounding areas, whose abundances may be roughly determined by reports of damage and insect outbreak records.

A few remarks on the general features of such a project may not be out of place here. It probably has been rather obvious throughout the text that one of the chief difficulties encountered has been the lack of any standard or even comparable means of recording outbreaks. For the most part this study has been based upon old inadequate observations which, while of value as a rough index of what has been going on as regards insect fluctuations in the past, cannot be considered as being very precise and exhaustive. It is imperative, therefore, if we are to attempt to study the natural fluctuations in populations of insects—be they economic or not—to revise completely our methods of observation. It is not sufficient to record the years when an insect has been

"injurious", for this is a very subjective and elusive adjective. Some estimation of the actual numbers and density of the individuals of each species is necessary.

A word as to possible methods. Perhaps some of the best and most extensive studies on population fluctuations over large areas and which offer certain suggestions here, are those carried on by the Bureau of Animal Population at Oxford. Here is being conducted a large-scale study of fluctuations in the populations of the fur-bearing mammals of their Canadian wild life enquiries and a similar study on the game-bird populations in Britain. The general comparative method adopted in these studies might well be adapted in such a large-scale survey of insect populations: a survey involving, not the "plus" and "minus" years of injury, but fluctuations in the actual or estimated numbers or both on a running curve over many years. Standard methods and criteria of obtaining data would have to be set up; for example, observations should be made in comparable habitats and vegetation in equivalent seasons. It would be well to start with species of certain and easy field identification in order to determine the most practicable methods to be used. A system of questionnaires and illustrated leaflets assisting in field identification (along the same principles as those used in the bird-banding and the butterfly migration studies) could be circulated among agricultural agents, amateur naturalists and the more scientific farmers. These semi-amateur observations should be checked by well-trained observers, stationed at suitable points, who could correlate the other observations with their own which should be much more accurate and controlled. All observations and estimations should be checked by at least one other person, and due regard paid to such things as crop rotation and natural succession. While there should be more or less fixed stations for yearly and seasonal observations, there should also be sufficient overlapping of observations to counterbalance the above-mentioned features of crop rotation and succession. Such an organization could be adopted profitably in any of the agricultural countries and give much more utilizable results than those obtained at present. The similarity between the findings of Evans (1933, 1934) and those of Andrewartha & Steele (1934), working at Adelaide and Melbourne respectively (about 500 miles apart), on the abundance fluctuations of *Thrips imaginis*, shows what can be done by this method on a small scale.

For the time being, however, it should prove profitable to presume that the records of outbreaks which have been gathered together in this study are a fairly rough index of the abundances of insects throughout that portion of the past for which records are available, and should furnish the basis for a working hypothesis regarding insect population fluctuations. Perhaps the best indication that this assumption is not altogether an erroneous one is the remarkable degree of correspondence between the peak years for the various districts or regions into which the deciduous forest area of Europe was divided.

This would seem to answer, in part at least, the objection that we have no right to assume that the data are correct since they were originally collected by non-scientific persons who probably had no particular desire for accuracy. Another objection, perhaps more valid, is that the data are incomplete.

It is clear, then, that the graphs which have been presented give only a rough indication of the insect population present in any given year. An "outbreak" must, for the purpose of this study, be considered as being the time when insects of a given species are more abundant than usual, recorded because of an increased amount of noticeable damage caused by them. While the shortcomings of such an index are obvious, the fact remains that it is the only one we have. Presuming that the records have included the important outbreaks, a year in which there are twenty outbreaks obviously has more insect individuals present than a year in which there are only five. This, then, is our "index" of population density in this study.

In the first section a rough outline of the history of the recording of outbreaks was given. The gradual increase of the number of records each year has added to the difficulty of analysis and necessitated a sliding criterion for the determination of major trends.

In the second section the outbreaks of insects living in the deciduous forest area were dealt with. The vast amount of data necessitated a division of the area into smaller regions which was done on the basis of the geographic distribution of the records. In the cases of England and Poland, where intensive record keeping had thrown the data out of line with the general run of records, the data were considered separately from the rest. On comparing the "peak years" in the various districts and countries considered separately, there was found to occur a correspondence which indicated general trends of abundance throughout the entire area. These trends, or peaks of widespread existence, did not recur at regular intervals, but appeared to be present in a slowly diminishing regression in which the time between the peaks diminished from about 12 years in 1780 to about 6 years in 1915. A similar, but less definite, regression was found in the study of the years of greatest locust migrations in section 4 (*c*). The earlier records being sporadic, summaries were made by 10- and 50-year periods; these showed the presence of major fluctuations which had some correlation with similar major fluctuations in China.

In the third section were considered biotic areas in the U.S.S.R. other than the deciduous forest, i.e. the taiga, forest-steppe, steppe, semi-desert, and the Caucasian forest area. For these areas the records are much less abundant and do not include much more than the last 40 years. On comparing the recurrences of abundance of insects in these regions, the total area of which is less than that of the deciduous forest, one finds less correspondence between the peak years than was found for the subdivision of the deciduous forest area, although in certain years a trend is apparent throughout all biotic areas.

From this it may be concluded that some major influence, presumably climate, operates throughout all areas, and that particular trends are more widespread than others, the latter being more or less restricted to one given biotic (and climatic) area.

Two insects which repeatedly appear in large numbers in the deciduous forest area were considered separately for individual reasons. The first, *Melolontha*, because its 3–4–5-year cycle has caused a number of "outbreaks" to be recorded when these dates were most probably only the usual flight years for the insects. A Swiss study, however, has presented records of actual collections of adults over a number of years, and this reveals fluctuations which did not correspond with those of the deciduous forest area; however, as we have seen, it is not unusual for the abundance periods of a single species to differ from those of the population as a whole.

The other insect, the migratory locust, has been discussed so frequently elsewhere that only a brief discussion of its general migration periods and routes was made. There were found to be both major and minor trends of recurrences of abundance in countries other than the breeding areas, neither of which could be said to occur regularly. In Tables 5 and 6 is given a comparison of the major and minor trends of the different areas used. In the former are included the major trends in the European deciduous forest areas, and the abundance periods of locusts in Europe. There appear to be several major groupings into which these recurrences may be divided: 1780–1880 (–1915?), 1680–1760, 1445–1655, 1290–1405 and 1120–1250, although the significance of these divisions, if any, is obscure.

Thus far the discussion has been centred upon the trends of fluctuation of the population as a whole, i.e. of many species considered together. In analysing the peaks it was found that certain species tended to occur in outbreak conditions more frequently during the total population abundances than others and hence were more characteristic of the fluctuation pattern of the region, although none was consistent in its behaviour in this regard. However, in more than half the cases for the insect species records which were complete over fairly long periods of time, there was found to be some change in their abundance about the time when total populations were at their maximum: both decreases and increases were observed. The exact nature and possible causes of this is possibly explainable in terms of biotic balance, but the details are not clear.

Summarizing, the following observations may be made in light of what has been shown above:

(1) There is a very evident tendency for insect outbreaks to be more numerous in certain years than in others, i.e. they behave as normal fluctuations of animal populations.

(2) There is no definite periodicity in the recurrence of these peak years of outbreak abundance. There has possibly been a regression in the interval

Table 5. *A summary of major fluctuations*

General insects in Europe	Locusts in Eurasia
1871–1880	
1831–1840	1780–1880(–1915?)
1781–1800?	
	1680–1760
1526–1550?	1525–1580
1476–1500	1445–1505
1376–1400	
	1290–1405
	1120–1250

Table 6. *Conspectus of peak years of outbreak abundance in all areas studied; years with dubious peaks designated by (?). This table indicates what are termed "minor fluctuation trends" in the text*

Deciduous forest							
All	Pre-1850 spp.	Taiga	Forest-steppe	Steppe	Semi-desert	Caucasian forest	Locust peaks
—	—	—	1933	—	—	—	—
1931	—	—	1931?	—	—	—	—
—	—	1929	—	—	1929	1929?	—
1928?	1928	—	—	1926	—	1927	—
1924	1924–5	—	—	1924?	—	1924?	—
—	—	1923	1922	—	1923?	—	—
1921?	1921	—	—	1920	—	—	—
1917?	1917	—	—	1917?	1917?	—	—
—	—	1915?	1914–15?	—	1914?	—	—
1913	1912	—	1912?	1912	—	1912	—
—	—	—	1910	—	—	—	—
1908	1908	1908?	—	—	—	—	—
—	—	—	1907	1906	—	1906??	—
1902	1902–4	—	1903	1902	—	1902	—
—	—	—	1901	1900	1900	1900	—
—	—	1898	—	—	—	—	—
1896	—	—	1896	1896	—	—	1895
—	—	1894?	1894?	—	—	—	—
1892	1892	—	—	—	—	—	—
1888?	1886	—	—	—	—	—	—
1883	1883	—	—	—	—	—	—
1875	1875	—	—	—	—	—	—
1872?	—	—	—	—	—	—	—
—	1870	—	—	—	—	—	—
1869	—	—	—	—	—	—	—
1863	1862	—	—	—	—	—	—
—	1857–8	—	—	—	—	—	1855
1854	1853	—	—	—	—	—	—
—	1846	—	—	—	—	—	—
—	1837	—	—	—	—	—	—
—	1828	—	—	—	—	—	—
—	1818	—	—	—	—	—	1815
—	1809	—	—	—	—	—	—
—	1797	—	—	—	—	—	—
—	1784	—	—	—	—	—	1785
—	1769	—	—	—	—	—	—
—	1755	—	—	—	—	—	—
—	1744	—	—	—	—	—	1745
—	—	—	—	—	—	—	1715
—	—	—	—	—	—	—	1695
—	—	—	—	—	—	1165?	1635?
—	—	—	—	—	—	1095?	1545
—	—	—	—	—	—	935??	1475
—	—	—	—	—	—	885	1405?
—	—	—	—	—	—	695	1335
—	—	—	—	—	—	595	1245?
—	—	—	—	—	—	—	1205?

between peak years, and a more definite tendency for some longer time-groups (25- or 50-year periods) to have more outbreaks than others.

(3) The fluctuation in the number of yearly outbreaks is a general phenomenon over a large area, occurring synchronously throughout the entire area of the deciduous forest region of Europe. This is shown by the agreement of the fluctuation patterns of the subareas into which the general area was divided.

(4) A comparison of the fluctuation patterns characteristic of the deciduous forest area with those of certain other biotic areas (taiga, forest-steppe, steppe, and semi-desert), shows that while certain master trends are present everywhere, the fluctuation pattern is more or less distinctly different for each biotic area and is probably characteristic of each individual area.

(5) There therefore appears to be a general reaction in time by the entire insect population as a whole.

(6) While the fluctuations characteristic of the population as a whole cannot be characterized by any individual species, there is evidence to show that in years when there is a larger insect population there is a considerable upsetting of the biotic balance, as is shown by the change (either by increases or decreases) in numerical abundance in species which characteristically have "prolonged" periods of outbreak.

7. Review of opinions on outbreaks, and conclusion

The general subject of cycles has been discussed in section 1, but several interesting cycles may be noted. Jünger (quoted in Schnauer, 1929) gives a general outbreak cycle whose peaks are 1700, 1740, 1780, 1815, 1850, 1880 and 1920. This agrees with the findings of the present study inasmuch as our corresponding peaks occurred in 1743, 1783, 1818, 1853, 1883 and 1924. However, our long periods of greatest insect activity have little in common with Jünger's cycle.

Eidmann (1931) gives a graph for outbreaks of the principal German forest insects which agrees fairly closely with the findings of the present study. Gasow (1925) presents a climatic cycle upon which outbreaks of *Tortrix viridana* are indicated. The shape of fluctuation curves of individual species have been studied and commented upon by Bremer (1929) and Schwerdtfeger (1935).

It appears that the outbreak areas tend to follow certain natural regions, and this principle is held by a number of workers. As long ago as 1855 Severtzov touched upon the subject when he described a community as an "elementary fauna". In Germany, Börner and others (1921), Friederichs (1927), Schnauer (1929) and Schwerdtfeger (1935) have emphasized the importance of taking into account the natural regions and ecological habitats, when dealing with outbreaks. In America Shelford (1929), Howard (1927), Huber & Neiswander, (1927), Transeau (1927), Cook (1929) and Sweetman (1933) have emphasized the importance of regional factors in the habitat of organisms and their populations.

Natural conditions are held by some to be less prone to outbreaks than the conditions of "pure stands" of single plant species. Eidmann (1934) suggests that a return to natural conditions in the German forests (in place of the present habit of planting forests of single species and harvesting the entire crop at one time) should decrease the number of insect outbreaks. Brues (1923) remarks: "Only very exceptionally do natural associations of plants offer ideal conditions for monophagous insects.... Under natural conditions, as they existed before agriculture changed the face of nature, there can be little question that insect species of polyphagous tastes were represented by larger populations than those affecting more restricted diets for it is only under very exceptional conditions that natural associations of plants are sufficiently dominated by a single species of plant to offer ideal conditions for the multiplication of monophagous insects." As I have shown elsewhere (1936), annual and daily fluctuations in insect numbers present in the vegetation strata are less intense in climax communities (prairie and forest), than in subclimax communities.

Endemism is usually not considered as an important element in outbreaks, but it would seem that it is only in areas where an organism is usually present that it can have a true outbreak. A species may attain a state of abundant endemism in one portion of its range (i.e. where it is noxiously abundant at all times), be recurrently abundant (epidemically) in another, and periodically invade new or marginal areas in large or small numbers. The instances cited by Uvarov (1931, pp. 158–9) are the Lepidoptera *Colias croceus* Fourc. and *Acherontia atropos* L. which extend their northern European range every 11 years (?). Migratory locusts are an example *par excellence*. This idea is not new (see Cook, 1929), but it may be used to distinguish between invasions (English sense) and outbreaks; the latter probably only occur in the second region, although an interesting case is cited by Blackman (1924) of an instance of the beetle *Eccoptogaster quadrispinosus* Say, where this bark-beetle started increasing in 1912 and continued gradually until 1915 when it assumed outbreak proportions. In 1916 it resumed its 1914 abundance and increased steadily until 1923 when it was considered as a serious endemic pest. Here we have an instance of a rise to endemism by a former none too abundant species, undergoing an outbreak while so doing.

Although climate is usually given much emphasis in the question of outbreaks, another important factor is physiology. Although no definite statement can be made on the subject, it is very probable that in some cases at least there is a change in physiological conditions at times of outbreak. The effect of crowding in certain grasshoppers is known through the work of Uvarov (1928), Vayssière (1931) and Faure (1932); here, apparently, there is an increased rate of metabolism, as is evidenced by the change of coloration as well as in behaviour. Similar effects have been noted in many non-swarming grasshoppers by Rubtzov (1935). The multitudinous effects of crowding in other animals have been reviewed admirably by Allee (1931).

There are several recorded instances of change in reproduction rate during the course of outbreaks, which may or may not be correlated with crowding. Voelkel (1930) observed that the number of eggs and the size and weight of pupae increased before an outbreak and decreased thereafter; he further noted that if an injurious factor interfered with the larva after the peak of abundance had been reached, the rate of decrease was accelerated in subsequent generations; the data for his conclusions have not yet been published. Grossgeim (1930) also observed fluctuation in reproductive capacity of the females and attributed outbreaks to this cause. The *Review of Applied Entomology* abstracts the views of Nechleba (1927) as follows (1928, 16: 4): "Among the factors ending outbreaks of forest pests must be included the gradual decrease and cessation of reproduction noticed once a pest has reached its maximum abundance. Although this phenomenon may be closely connected with other causes, such as polyhedral disease in the case of *Lymantria* (*Liparis*) *monacha* L., until fully investigated it must be regarded as an independent factor. This decrease in power of potency occurs in various insects.... Instances are quoted relating to *Porthetria* (*Liparis*) *dispar* L., *Lymantria monacha*, Tachinid flies, and the Scolytid, *Myelophilus piniperda* L.)." A somewhat similar phenomenon has been noted by Shelford (1932) who remarks (p. 545) that "the success of the [chinch] bugs [*Blissus leucopteris* Say] in a long series of cultures [under laboratory conditions] shows that their vigor varies from year to year. The bugs were very strong in 1919 and 1925, producing 3 or 4 generations in each of these years. They were weakest in 1921. This does not, however, correspond with the severest outbreaks of the bugs in the state [Illinois]. It does indicate the possible importance of internal factors not directly correlated with the immediate surrounding conditions but determined earlier. It is necessary to consider *unbalance* in the bugs themselves as well as the *unbalance* in the system of which they are a part."

A suggested "function" of an outbreak for certain species has been that it includes a physiological ridding of the race of certain characteristics and weaknesses which have accumulated. Cook (1929) observes that the moth *Porosagrotis orthogonia* Morr. must have an outbreak in certain areas of its total range at least once every ten years, or else it dies out and the area must be re-invaded by new individuals from the more densely populated area.

The fluctuation in the physiological conditions of host plants of many species frequently cause fluctuations in predator abundance. Lees (1926), Cutright & Huber (1928) and Davidson & Henson (1929) correlate insect damage with the vigour of growth and condition of the host plants; while Mumford & Hey (1930) relate the water balance within the plants to their resistance to attack by sucking insects. Other examples might be cited.

Concerning environmental factors and their effects on outbreaks much has been written; an excellent summary of the subject has been prepared by Uvarov (1931). Many economic entomologists have based their explanations for outbreaks on the immediately preceding climatic or local conditions and

have largely ignored the possibility of biotic interactions, internal physiological conditions, and the like. The importance of natural conditions in discouraging outbreaks has been emphasized above. The subject of parasites and their effect may be found discussed in many accounts on "natural control" of insect pests; in this connexion the reader is referred to the papers of Burgess (1926), Catoni (1914) and Friederichs (1932) as representative studies on parasite abundance in periods between or during outbreaks.

Parasites represent an important phase of biotic interaction, and it is usually in the predator-prey relationship that one is likely to think of community interrelationships. A similar reaction of species within the same niche (i.e. possessing similar mores) is well illustrated by the phenomenon of concurrent outbreaks within a given area. I have noticed 28 instances of insects (not including grasshoppers, where many more instances may be found) outbreaking synchronously within a given area, and attention called to the fact in the reporting article. A study of these instances gives the following observations:

(1) Ecological (probably environmental) conditions have been present stimulating more than one species into outbreak proportions at one time. (2) The possibility of any "innate" rhythm increasing in two or more species (more or less distantly related) at about the same time seems to be assuming more than the available evidence warrants. (3) Concurrently outbreaking species may be considered as having certain mores in common, and in many instances (e.g. grasshoppers) fall into the same ecological niche in the area. (4) In these concurrent outbreaks it is frequent that one species is more abundant than the others. But in subsequent outbreaks in the area the same species may not always be in the lead, one of the former subordinate species taking the place of greatest abundance. In different areas different species may assume the major rôle, and the major species of one area may be a minor species in another at outbreak time. In one instance reported by Corkins (1922), a grasshopper outbreak in Colorado had a great preponderance of *Dissosteira longipennis* on the uplands and *Melanoplus bivittatus* and *differentialis* in the valleys (cf. also Davidson, 1932, p. 309 and Parker, 1933). These and other instances lead one to the contention that certain outbreaks may be considered as being an ecological phenomenon of the niche rather than pertaining to the component species.

In several of the instances cited above the facts could be interpreted on the basis of mutual exclusiveness, a phenomenon frequently found but not always correctly interpreted. Mutual exclusiveness may lead to a lack of active competition, and Corkin's example of the three grasshopper species is an instance of this case. Eidmann (1934), in comparing the frequency of outbreaks of the Kieferspanner (*Bupalus*) and the Forleule (*Panolis*), showed that in the area he studied there had been no outbreak of both species at the same time during the past 100 years. In Mecklenburg (Friederichs, 1933)

areas infested with *Panolis* coincide with those of *P. monacha* (the nun moth), but no mention is made of synchronous outbreaks. Konakov (1930) reports that *Phytometra gamma* and *Loxostege sticticalis* outbreaks do not coincide although both species feed on the same plants in the same areas.

Coordinate with "concurrent" outbreaks is the item of "sequence" outbreaks. These latter may be due to two causes: simple ecological succession on a large scale, or a lag in one species in response to an initial cause which originally stimulated the general outbreak. Of this type there are 9 references at hand.

To be considered under *the ecological position of the organism in the community* are the factors of (*a*) the presence, abundance and periods of activity of the particular organism's competitors for its basic requirements, and (*b*) the presence, abundance and activity periods of its present or potential predators, parasites and diseases. It is necessary also to consider *the ecological stability of the community*: here are involved the factors of (*a*) the ability of the habitat which the community occupies to buffer it from the rigours and sharp changes in climate; (*b*) the community's susceptibility to, and ability to resist, invasion by (1) invaders from a community of more climax rank, (2) periodic (i.e. seasonal) invaders, and (3) sporadic invaders, i.e. those from other areas brought in by the sporadic instability of other habitats (e.g. locusts, nutcrackers); and (*c*) the presence and degree of internal "unbalance" fluctuations on the part of its associated organisms which are due, in turn, to the stability or instability of their ecological position in the community. Also to be considered here are the items of the presence and permanent availability of the basic necessities of food and the requirements for carrying out the fundamental life processes. Likewise important are the items involved in *the physiological vigour of the species*: the variability in its general vigour, the variations in its reproductive and viability rates, its general "environmental resistance", as well as the resistance and fluctuations in physiological vigour of the hosts—be they animal or plant—upon which the organism feeds. It is also necessary, if any organism is to obtain the status of great abundance, that the time of potential mass increase should coincide with the period when the resistant elements of general environment—ecological as well as physical—should be at a minimum. If a portion of the life history is spent under different conditions from that of the rest, the organism must be able to find a reasonably nearby area where it may again find its basic requirements for existence there as well as being able to "fit in" with and obtain an ecological place in the second community as well.

It is therefore obvious that a complex of biotic interaction and balance or unbalance ultimately governs the numbers of individuals of any species which may exist in a given area at any time. The problem is made no easier by the fact that all insects are not equally active during the same times of the year. Were the climate to remain stable over a period of years (and man not interfere

by a change of crop ratios), it is probable that the number of "outbreaks" would gradually decrease. But climate shows no tendency to remain stable: its periodic and sometimes erratic pulsations serve as an inopportune "meddling" with the swinging of the biotic pendulum. Man, too, shows no inclination to cease his interference of the unbalance of nature with his introductions and his "regulating" of the densities and varieties of communities present.

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9. Summary

1. Although no sufficient census data exist for the determination of long-term trends in insect populations, the published records of insect outbreaks can be used to give a rough measure of periods of abnormal abundance in certain species.

2. These records were compiled for a large part of Europe and analysed in regional groups which follow broadly the natural vegetation regions.

3. A brief description of each of these natural regions is given. An analysis of the records of insect outbreaks in them suggests that, in the deciduous forest region at any rate, outbreaks tend strongly to occur in the same groups of years, or are nearer together than would be expected from chance.

4. This conclusion rests upon admittedly unsatisfactory field data, and the importance of testing it by means of more objective measurements of sample populations is stressed. A review of some of the present systems by which outbreaks are recorded officially in different countries, gives point to this suggestion.

5. If the synchronization of outbreaks is a reality, it can be explained in various ways. It is suggested that the outbreak of one species may cause disturbances in the community which may generate similar outbreaks in other species. Some instances of disturbance by invaders from outside (e.g. locusts) are discussed.

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(Many references used in obtaining the recorded data are omitted from this bibliography because of lack of space. A manuscript copy of the text, data, and bibliography of all references used is filed in the Library of the Bureau of Animal Population, Oxford University, England, and another copy in the Library of the Zoology Department, University of Oklahoma, Norman, Okla., U.S.A. Photomicrographs are obtainable at cost price from the latter institution, by application to the Librarian. All the references containing data are listed in the *Review of Applied Entomology*, Series A.)

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REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 28, No. 1, February 1940)

This number contains 11 original papers, two book reviews and some notices of vegetation. In addition, there are the Secretary's and Treasurers' Reports of the British Ecological Society for 1939, notices of the Society's meetings and a list of members.

The considerable interest recently shown in Arctic vegetation is illustrated by three papers dealing with different aspects of this subject. P. Falk contributes a further detailed study on the ecology of an area in Central Iceland, with particular reference to soil movements. A. M. Acock gives an account of the vegetation of a calcareous inner fjord region in Spitsbergen, drawing attention to the influence of the calcareous soil and of other edaphic and climatic factors. R. Scott Russell describes the vegetation of Jan Mayen Island in the first of a series of ecological and physiological studies.

Papers on British vegetation include one by A. R. Clapham on the role of bryophytes in the calcareous fens of the Oxford district. A fifth instalment of studies on the ecology of Breckland by A. S. Watt deals with the grass-heaths and their degeneration towards a form of lichen-heath. J. L. Harley gives a study of the root system of the beech in woodland soils, especially from the point of view of its mycorrhizal relations. R. W. Butcher summarizes two years' data on the algal ecology of the River Hull. Bearing also on methods, is a paper by J. F. Hope-Simpson illustrating the possible errors in the "subjective frequency" method of describing vegetation, by data drawn from chalk grassland.

The three remaining papers consider various aspects of vegetation abroad. V. J. Chapman in the sixth and seventh of his studies in salt marsh ecology, considers the vegetation of salt marshes in the Eastern United States. N. C. W. Beadle gives records of the soil temperatures found during forest fires in Australia and of the morphological features of species able to withstand fire damage. A paper of particular interest and importance to colonial foresters deals with the methods of recording the structure, life forms and flora of tropical forest communities as a basis for their classification. This, prepared by P. W. Richards, A. G. Tansley and A. S. Watt, is reprinted from a bulletin of the Imperial Forestry Institute.

Reviews deal with books on the British vegetation and on the Californian Flora. A long list of titles of papers on the ecology of bryophytes is contributed by P. W. Richards.

W. H. PEARSALL.

AMERICAN ECOLOGY

Frederick E. Clements and Victor E. Shelford (1939). *Bio-ecology.* 425 pp., many text-figures, maps and photographs. John Wiley and Sons, Inc., 440 Fourth Avenue, New York, and Chapman and Hall Ltd., 11 Henrietta Street, London, W.C. 2. Price £1. 2*s*. 6*d*.

When the leading plant ecologist and the leading animal ecologist of a country combine to write a book which expresses to a great extent the sum of their conclusions over a lifetime's work, no ecologist can omit to study them with more than usual care. In doing so he will bear in mind that Clements and Shelford were both pioneers in the subject, and have probably contributed far more to the hidden structure of his ideas than can be realized at all easily. And whether he disagrees with some of the conclusions or not, it has to be remembered that a generation of American students has grown up under the influence of

these ideas, and has been taught to investigate the wonderfully rich and fascinating fauna and flora of their country with an entirely new standard of careful measurement and a synthetic attitude towards wild life.

From this book on ecology it is easier to find out what the authors believe than what the evidence is for these beliefs. Their most important tenets seem to be that plant communities can be arranged and classified in a logical manner according to the trends of ecological succession, and that animal communities must be studied as integral parts of a whole complex of plants and animals—and that they accordingly fit into the same plan of classification. While it is well known that many British ecologists will not go as far as Clements in dragooning plant communities into stages and exact trends, there is no substantial criticism of the first part of the theory. For practical purposes, plant succession is a true and useful concept. But we cannot be nearly so certain about the relation of animal to plant communities. No one has ever denied that animals depend upon plants, and plants upon animals, in a multitude of ways that make the plant-animal cosmos into a closely bound system—bound equally closely, as Tansley has pointed out, with the physical environment in which they live and which flows into and out of their organisms perpetually. The real question confronting us is whether animal populations are so distributed between different habitats, especially those well-marked habitats produced by plant dominance, as to exhibit any limited organism-like behaviour similar to plant communities; and if so whether such quasi-organisms coincide at all closely in their distribution and the boundaries of their influence on neighbouring systems. On this question the book offers no real evidence, although a belief in the identity of plant and animal community distribution among habitats appears to underly much of the argument put forward.

In many ways the book is a difficult one to review, indeed to read consecutively. It abounds in so many technical terms that one has always wished to shun (for instance "inter-relation" becomes "coaction"; there is the really horrible word "coactee"; "disoperation", for harmful results of crowding). The word "ece" (for "habitat") is strongly recommended by the authors, but only used occasionally. Were it not that populations of human students in America are being taught to use these unnecessary and pedantic terms, so that the thought of a whole country is to that extent clogged with them, one could afford to treat them as mild aberrations of the authors, similar to a passion for writing diaries or collecting curios. Were it not that one knows for an absolute certainty that the authors are men of real greatness and brilliant insight into natural phenomena, one would scarcely be able to tolerate the stilted nature of the language, or the implication of certitude and finality that the terms convey. However, as an Indian proverb says: "One can stand being kicked by both hind legs at once if only the cow be a good milker."

The substance of the book is discussion of various aspects of community structure and relationships, followed by three special detailed sections which describe (1) the North American grassland communities, (2) Aquatic (fresh-water) climax communities, (3) Marine communities, pelagic and bottom. In the first half of the book, the discussions bring out many relationships, of which perhaps the most interesting to animal ecologists will be the effects of animals upon plants and upon the conditions in which plants live. They centre round the main idea that: "The biome or plant-animal formation is the basic community unit; that is, two separate communities, plant and animal, do not exist in the same area." Much useful work is summarized, some of it with really good diagrams and photographs. The ecologist may be advised, first to learn the peculiar language in which the discussions are couched, then to ponder deeply over the evidence, and see whether it would not be possible to devise some field statistical observations that might clear up some of the points at issue. There is quite a large section devoted to fluctuations in communities and populations, which gives about the best critical summary of major animal cycles that has been published.

The three special sections make pleasant and absorbing reading, and the very large bibliography (including a good deal of European, but not very much British, work) is valuable. In fact, the remarks I have made in this review, might draw attention away from the very rich learning and acquaintance with plants and animals under natural conditions, which the text displays—a learning that ranges over the whole world. CHARLES ELTON.

ECONOMIC INSECTS

C. L. Metcalf and W. P. Flint (1939). *Destructive and useful insects, their habits and control.* 2nd edition, 9×6 in., pp. xvi+981, 584 text-figures. McGraw-Hill Publishing Co. Ltd., Aldwych House, London, W.C. 2. Price £2. 10*s*.

This edition contains about one-fifth as much material again as does the first edition and has been so extensively revised in order to bring the text in accordance with present entomological practice that it is virtually a new book. The first eight chapters are introductory in nature and include descriptions of the essential features of the morphology, physiology and development of insects, a survey of the various orders and keys for identification of winged and apterous adults, *nymphs, larvae and pupae*! Chapter 9 discusses the various kinds of control measures now in use, e.g. chemical, mechanical and physical, cultural, biological and legal, and Chapter 10 describes and figures numerous insecticide appliances. It is the latter half of the book from Chapter 11 onwards which will be of most interest to ecologists. Here some 350 species, arranged in groups, according to the crop or animal attacked, are fully discussed from the point of view of importance, type of injury, identification, life history, habits and control. A welcome feature is the provision at the commencement of each chapter of a field key which should enable one to identify pests from the immature stages and the type of injury they cause even in the absence of the better-known adults. As Dr C. B. Williams has pointed out in an amusing article on "The duties of an administrative entomologist" (1927, *Scientific Worker*, 5: 36), when dealing with a pest one should know "when to attack direct, when to attack indirect, and when to 'lie low an' do nuffin'". The selection of the most appropriate method is only possible after a detailed study of the life-history and ecology of the pests has been made, and the progress attained in such investigations since publication of the first edition, and incorporated in the present volume, is one of the most striking things about it. A few examples chosen at random from the chapter on insects injurious to corn are given to demonstrate how frequently ecological considerations determine the method of control.

Grasshoppers: "The bait should be applied early in the morning as this is the time of heaviest feeding of the grasshoppers."

Armyworm: "Because of their habit of feeding at night, their presence is generally not suspected until the crop is nearly destroyed. . . . The bait should be spread in the late afternoon or early evening."

Fall Armyworm: "Cold, wet springs check the parasites more than they do the insects that they feed upon. In such seasons, especially, watch should be kept of grassy fields for the appearance of the young worms. . . . Fields in which they have been feeding should be disked or otherwise lightly cultivated. . . to break up the pupae and throw them out on the surface, where natural enemies and weather conditions will destroy many of them. Keeping fields of cotton and corn free from grass will do much to prevent injury by this insect, since the infestations almost always start among grasses."

Cutworms: "Summer plowing, before the eggs are laid, and fallowing until frosts occur are of value against all species which lay their eggs upon low-growing vegetation."

Chinch bug: "One of the most effective methods of combating the chinch bugs is trapping them at the time of small-grain harvest when they are travelling on foot from small-grain fields to fields of corn or other growing grass crops."

Southern corn-stalk borer: "As the insects hibernate in the stalks of corn and other food plants, a thorough cleaning up and burning of cornstalk refuse and corn stubble, immediately after harvest, is the most effective control measure."

Corn root aphid: "The best and most effective method of combating these aphids is a measure directed, not against the aphids, but against their attendant ants. This consists of thorough deep cultivation of the soil early in the spring before planting. . . . The object. . . is to break up, scatter, and destroy the ant nests in the soil."

Although written primarily for agriculturalists in the United States and southern

Canada, the book contains much general information applicable to economic problems in any part of the world and should, therefore, enjoy a wide circulation. It is profusely illustrated and well documented, and, like all McGraw-Hill publications, is well printed and strongly bound.

B. M. HOBBY.

SCHOLASTICISM IN ECOLOGY

Plant and animal communities: comprising the Proceedings of the Conference on Plant and Animal Communities, held at the Biological Laboratory, Cold Spring Harbor, Long Island, New York, from 29 *August to* 2 *September* 1938. Edited by **Theodor Just.** Reprinted from the American Midland Naturalist (1939), Vol. 21, No. 1, pp. 1–255. Published by the University of Notre Dame, Notre Dame, Indiana, U.S.A. Price $2·50, post free.

Ecology has come to the stage at which the enormous scope and ramifications of the subject can be dimly seen, and also the need for some kind of system for classifying information about communities upon a common plan. Yet we still have very little reliable information upon which such a classification can be made. Differences of locality and history, and the natural instability and flexibility of organization of animal and plant communities demand a tremendous sustained effort of field study and the organization of raw data which ecology, specially animal ecology, has simply not yet attained, before a permanent and true classification can be erected.

It is natural, however, that serious ecologists should meet to discuss this state of affairs and put forward their ideas about the relative value of various concepts and the standardization of technical terms. The Conference at Cold Spring Harbor covered a wide range, but had as its background the aim of introducing some agreed order into ideas about the nature and classification of ecological communities. In the Editor's words: "the book tries to bridge the wide gaps existing particularly between the cis- and transatlantic ecology, between the botanical and zoological aspects, and to establish once more the common needs and problems." No one who has read recent text-books and papers will disagree with the worthy aims here expressed. (Incidentally, what about standardizing the meaning of the terms cis- and transatlantic!)

There are ten contributions. Those by Conard, Gleason, Lippmaa, and Cain are concerned with plant communities; those of MacGinitie, Eggleton, and Carpenter with biotic communities (the first in the sea, the second in fresh water, and the third with communities in general); those of Emerson, Tinbergen, and Thomas Park with social organization and population problems in the animal community. Such a cross-fire from plant and animal ecologists produces naturally a great deal of interesting information and ideas. It is a pity that the discussions after the papers have been so mutilated by the Editor's necessary condensation as to be often meaningless.

This symposium carries a slightly unreal atmosphere with it, on account of the firework display of grand-sounding terms descriptive of the community and its constituents and their interactions, which might mislead the reader into thinking that something really solid was already known about these subjects. The truth is far from this desirable condition: we have as yet practically no quantitative data about animal (even plant) communities and their dynamics, of any general validity. For example, there is little information in existence about the natural rates of increase and mortality in nature of any plant species; or of the exact nature of the junction between the animal communities or populations inhabiting two major plant-dominated zones.

The Proceedings resemble an account of a reception at which only persons with the most impressive names were allowed to take part (I refer here metaphorically to the technical terms which have been admitted—not, of course, to the accomplished ecologists who attended the Conference). Some rooms are closed off with the notice: "Facts not admitted"; others are labelled "Reserved for internal operations, reactions and coactions only". Words like "fundamental", "lentic and lotic communities", "superorganismic" and "lociation" echo

across the crowded chamber. For a short space, everyone can be happy. We feel that after about a quarter of a century's preliminary fact-finding (and not a little important fallacy-finding) the ecological scholasts are getting seriously down to work, in their own fashion, to put the ecological house in order.

But, when one enters the field and begins to nibble at the edge of vast and subtle wild life problems, how much use are all these terms and concepts at the present stage of our knowledge? Are they not just of sufficient use to prompt one to undertake some fresh and unhampered field studies, which may reveal the real shape of nature, rather than confirm a shape which has been already crystallized in the class-room or conference chamber? Having fought a losing rear-guard action for fifteen years against scholasticism in ecology, I am not surprised to see the growing rigidity of ecological concepts, born of the natural human need for certainty. But I am still very doubtful whether these elaborate systems of relationship, with their uncouth bastard classical names, are in the majority of cases underpinned by a sufficient body of field records.

The tendency to teach ecology to students in a formalized way, is naturally greater in a country which includes the subject in University courses, and has to fit its methods to the requirements of formal examinations. Let us admire the progress which America has made in this direction. If ecology ever becomes widely taught in Great Britain, no doubt the same tendency will show itself. But, on the whole, it seems that far too much effort has been put into the organization of terms and concepts, and far too little into the accessible arranging of our existing body of ecological records.

Although there is much good stuff in all these papers, veiled though it is to some extent by the prevalent passion for cryptic and seldom euphonious terminology, I would single out the last one, by Thomas Park, on "Analytical population studies in relation to general ecology" for its sensible and constructive tone, and after it the papers by MacGinitie on "Littoral marine communities" and by Lippmaa on "The unistratal concept of plant communities" for the originality of their contents. CHARLES ELTON.

SHORT REVIEWS

Orlando Park, W. C. Allee and V. E. Shelford (1939). *A laboratory introduction to animal ecology and taxonomy. A laboratory guide with keys prepared with particular reference to fresh-water and terrestrial habitats of the deciduous forest region in North America.* 273 pp. and 17 text illustrations. The University of Chicago Press, Chicago, Illinois, U.S.A. (also through Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1). Price $2·00.

This interesting book consists of fairly small pages with iron hoops looped through them in loose-leaf fashion, apparently to allow the pages to lie flat easily during laboratory work, and perhaps to allow of easy revision in later editions. It contains three elements, of which the taxonomic with its careful keys and descriptions is by far the largest. The scope is clearly indicated in the subtitle of the book. Something of the sort for the deciduous forest zone of Europe (of which the British Isles are naturally an extension) is the British ecologist's dream. At present he has not even reliable handbooks and check-lists for a number of common animal groups—a condition of things that he is apt to attribute to a wicked conspiracy among systematists, but which is largely caused by the starvation of museums, and the poor training in taxonomy which is given to young zoologists in this country. There is an introductory part of the book, giving a brief summary of modern ecological ideas. This is well written and free from ecological cant. Under each group of animals there are suggestions for problems to tackle in the field and laboratory. These appear to be well-conceived and contain plenty of useful suggestions for teachers; but it must be admitted that a great part of their scope is simply that of zoology, as understood in this country. Much of it goes very wide indeed, e.g. into animal physiology. So much the better, provided a sufficient mental discipline can be maintained. There are a large bibliography, a glossary and good indexes. CHARLES ELTON.

N. B. Eales (1939). *The littoral fauna of Great Britain: a handbook for collectors.* 301 pages, 24 plates. Cambridge University Press, Bentley House, 200 Euston Road, London, N.W. 1. Price 12*s.* 6*d.*

Most students of zoology in Britain make a point of spending some part of their training period at one or other of the marine biological stations, and it is for them, in particular, that Dr Eales has written this book. After an introductory chapter in which she briefly considers the main factors in the zonation of animal life in the littoral habitat, and gives an interesting section on the status of each of the British marine biological stations, the main part of the book is taken up with a systematic account of the various animal phyla and their marine representatives. The descriptive matter dealing with the species themselves, or with the smaller classificatory groups, has been very carefully selected, so that the student will be able to identify nearly all the littoral species he may find with the help of the definitions and keys given. Each group is preceded by a short bibliography which will enable doubtful points to be referred to the standard systematic monographs. The illustrations, most of which are original outline drawings, are conveniently grouped in plates instead of being scattered at random throughout the text. Apart from supplying the needs of the student, this book will be welcomed for the efficient way in which it deals with the animals of a single habitat. Much ecological work in this country is held up by the lack of this type of book; perhaps others will follow Dr Eales's example. H. G. VEVERS.

Margaret Shaw and James Fisher (1939). *Animals as friends and how to keep them.* 271 pages, 22 text-figures and 16 photographs. J. M. Dent and Sons, Ltd., Aldine House, Bedford Street, London, W.C. 2. Price 6*s.*

Although this work is primarily intended as a popular book, whose aim is to put pet keeping on a more scientific basis and mitigate cruelty due to ignorance, it manages at the same time to be the complete *vade mecum* for the laboratory animal keeper.

Some 371 separate groups, species or varieties of animals are dealt with.

A huge collection of facts, many of them previously unpublished, is tabulated for each species or group under the headings of distribution, habitat, origin, description, length of life, care and food, housing, cage mates, behaviour, breeding, diseases, parasites, handling, transport, and cost (initial and upkeep), together with a section on "don't's" (as equally important as the "do's"), and a useful bibliography.

There are altogether 22 diagrams of cages and appliances.

Its application to ecology may not be obvious at first sight. Ecologists, however, are finding that it is essential for them to know more about the vital statistics of the life that they study in the field. Even superhuman watching will not reveal such things as the effect of age on reproduction or even much of the characteristics of age itself. Factors like these, of fundamental importance in the study of populations, can only be accurately assessed by the collection of data from animals kept in the laboratory under optimum conditions.

By the intelligent use of this book many new animals could be brought into the laboratory and successfully reared, and much valuable information about their functions, at present only obtainable from folk lore or by guesswork, would be learnt. R. M. RANSON.

Ann H. Morgan (1939). *Field book of animals in winter.* xv+527 pp., 257 text-figures, 26 plates (four in colour). G. P. Putnam's Sons, 2 West 45th Street, New York. Price $3·50.

This book deals with North American animals. Six general chapters precede those dealing with fresh-water sponges, hydras, planarians...through to mammals. The main knowledge summarized about winter behaviour is adequately shown in relation to that at other seasons, and quite considerable space is usefully given to group and species identification. The main impression is of interesting ecological and physiological discussions illustrated with good, clear diagrams and tapping the most relevant literature. DENNIS CHITTY.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Duplicate copies of these notices are no longer issued free with the *Journal*, but they can be obtained separately in stiff covers (printed on one side of the page to allow them to be cut out for pasting on index cards) from the Cambridge University Press, Bentley House, 200 Euston Road, N.W. 1, or through a bookseller, price 3*s.* 6*d.* per annum post free (at least 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, C. Elton, R. B. Freeman, B. M. Hobby, M. Mare, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern, H. G. Vevers and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND THE RELATIONS OF ANIMALS TO HABITAT CONDITIONS

(*a*) Marine and brackish

Tully, H. (1939). "Some further notes on the birds of the Northumberland coast in summer." Vasculum, 25: 83–7.

Brief notes on heron, sheld-duck, wood-pigeon, oyster-catcher, various waders, terns and black-headed gull. Suggests that there are more birds on the Northumberland coast than formerly.

Rudd, A. J. (1939). "The floods at Horsey: effects of the disaster of February, 1938." Salm. Trout Mag. No. 96: 255–61.

An account of the faunistic changes which occurred in Horsey Mere (Norfolk) after the sea broke through in February 1938. Most of the fresh-water fauna and flora was destroyed and marine fishes and Crustacea appeared. After the breach was repaired the salinity decreased and enormous numbers of *Gammarus zaddachi* appeared and were fed upon greedily by the returning fresh-water fish.

Hartley, P. H. T. & Spooner, G. M. (1938). "The ecology of the Tamar estuary. I. Introduction." J. Mar. Biol. Ass. U.K. 22: 501–8.

Description of the mudbanks, channel, tides.

Cooper, L. H. N. & Milne, A. (1938). "The ecology of the Tamar estuary. II. Under-water illumination." J. Mar. Biol. Ass. U.K. 22: 509–27.

Light penetration was studied with a Zeiss Pulfrich Photometer. The intensity of incident daylight is reduced to 1% at depths of 4 m. or less in the estuary.

Milne, A. (1938). "The ecology of the Tamar estuary. III. Salinity and temperature conditions in the lower estuary." J. Mar. Biol. Ass. U.K. 22: 529–42.

Rate of change of salinity may be of more importance than range, especially to some estuarine organisms. Rate, range and duration of fluctuation in salinity are greatest near low-water mark, least at high. Isohalines for a cross-section of estuary are shown. Friction at the edges makes salinities higher here on a falling tide than in mid-stream; lower on a rising tide.

Cooper, L. H. N. & Milne, A. (1939). "The ecology of the Tamar estuary. V. Under-water illumination. Revision of data for red light." J. Mar. Biol. Ass. U.K. 23: 391–6.

Fox, H. M. (1939). "Activity and metabolism of poikilothermous animals in different latitudes." Proc. Zool. Soc. Lond. A, 109: 141–56.

Blood-vessel pulsations in polychaetes and heart-beat rate in crustaceans were found to be roughly the same in English coastal forms and in Mediterranean ones showing adaptations to different temperatures, since raising of the temperature in the environment of the English forms to that of Mediterranean increased both pulsations and heart-beat rate.

Robertson, J. D. & Webb, D. A. (1939). "The micro-estimation of sodium, potassium, calcium, magnesium, chloride, and sulphate in sea water and the body fluids of marine animals." J. Exp. Biol. 16: 155–77.

A new method enables estimations to be performed on 1 ml. samples, with a limit of error of about 2%.

Fraser, J. H. (1938). "The fauna of fixed and floating structures in the Mersey Estuary and Liverpool Bay." Proc. Lpool Biol. Soc. 51: 1–21.

The relation of the flora and fauna to the unusual conditions of heavy sewage pollution, large salinity changes, instability of the bottom and the amount of silt in suspension is discussed. A series of floating structures affords a gradation to open sea conditions where a greater variety of species is found. Those species which are able to withstand the estuarine conditions thrive in numbers on the ample bacterial and phytoplankton food supply. Food chains are briefly indicated.

Russell, F. S. (1939). "Hydrographical and biological conditions in the North Sea as indicated by plankton organisms." J. Cons. Int. Explor. Mer, 14: 171–92.

A review of this important aspect of plankton work covers the subject since 1920. Indicator species of various "types of water" from different areas are listed and a generalized picture is drawn for the whole of the North Sea and coasts of the British Isles. Oceanic incursion is of first importance, since it may produce considerable enrichment of nutrient salts and thus may affect productivity for several years. Movements of rich and poor water, indicated in particular by *Sagitta* species, affect the survival of young fish, and may alter migration routes and distribution centres of fish. Further lines of investigation are suggested.

Fraser, J. H. (1939). "The distribution of Chaetognatha in Scottish waters in 1937." J. Cons. Int. Explor. Mer, 14: 25–34.

In a further contribution to the use of *Sagitta* species as plankton indicators, it is suggested that the variable characters of the same species may also be used as indications of the type and origin of water masses. Scottish data are correlated with those from Plymouth to show the probable cause of greater Arctic influence in the north in 1937.

Pierce, E. Lowe & Orton, J. H. (1939). "*Sagitta* as an indicator of water movements in the Irish Sea." Nature, Lond. 144: 784.

S. elegans is an oceanic form and predominates at Port Erin, Isle of Man; *S. setosa* is a coastal form and is only present from September to December. *S. elegans* only occurs at Liverpool from February to March. These interchanges indicate (*a*) extensive mixing of inshore and offshore waters in the greater volume and movements of the equinoctial tides, and (*b*) the occurrence of relatively stable bodies of water in Liverpool Bay in periods between the equinoxes.

Pettersson, H., Gross, F. & Koczy, F. (1939). "Large-scale plankton culture." Nature, Lond. 144: 332–3.

Describes the structure of, and preliminary experiments with, a twelve-metre vertical plankton shaft at the Vetenskaps- och Vitterhetssamhälle, Göteborg.

Rendall, R. (1936). "*Simnia patula* (Pennant) in Orkney." J. Conch. 20: 283–5.

S. patula, a Gastropod Mollusc, has not hitherto been recorded from the north of Scotland. The only other Scottish record is from the Sound of Mull.

Jones, E. W. Knight (1939). "A new record of *Phoronis hippocrepia* Wright." Nature, Lond. 144: 836.

Recorded as common on limestone boulders exposed in July and August spring tides, in the Menai Straits.

(*b*) Fresh water

Savage, R. M. (1939). "The distribution of the spawn-ponds of the common frog, *Rana temporaria temporaria* Linn., over a portion of the London Clay and associated drift." Proc. Zool. Soc. Lond. A, 109: 1–19.

A survey of spawn-ponds in the London area with a consideration of some of the factors affecting their selection. London Clay is unsuitable, possibly by the intermediacy of some chemical factor; potassium and carbonate ions are important, since frogs seek a rich concentration of the former and avoid a low one of the latter. The spawning migration is thought to be a definite purposive movement, as was shown by marking experiments.

Macan, T. T. (1939). "The Culicidae of the Cambridge district." Parasitology, 31: 263–9.

The mosquito fauna of cultivated fenland in the Cambridge district is compared with that of other districts, notably the natural fen at Wicken. Notes on the ecology and habitats of the various species are given. The habitat of the adult flies is related to the egg-laying habits of the female, the time of year at which oviposition occurs and her preference for damp ground or standing water.

Pearce, E. J. & Walton, G. A. (1939). "A contribution towards an ecological survey of the aquatic and semi-aquatic Hemiptera-Heteroptera (water-bugs) of the British Isles." Trans. Soc. Brit. Ent. 6: 149–80.

The various stretches of water examined are assigned letters indicating the vice-counties in which they are situated and numerals in order to distinguish them; these are followed by a brief description of their chief ecological features. The species encountered are arranged in systematic sequence; under each heading are included the key symbols identifying the place of capture, date, and sometimes indication of abundance. The authors appeal to collectors to assist in the preparation of further papers of a similar nature.

Walton, G. A. (1939). "Two water bugs new to Great Britain: *Microvelia pygmaea* Dnf. and *Microvelia umbricola* Wrob. (Hemipt.)." J. Soc. Brit. Ent. 2: 26–33.

Gives ecological details concerning the habitats of all the known British species of *Microvelia*.

Varley, G. C. (1939). "On the structure and function of the hind spiracles of the larva of the beetle *Donacia* (Coleoptera, Chrysomelidae)." Proc. R. Ent. Soc. Lond. A, 14: 115–23.

The spiracular hooks of the larva of this beetle are adapted to pierce the roots of aquatic plants; there is a channel through which gas can pass from the intercellular spaces of the plant to the tracheae.

Wingfield, C. A. (1939). "The function of the gills of mayfly nymphs from different habitats." J. Exp. Biol. 16: 363–73.

Experiments showed differences in gill function of mayfly nymphs from various habitats. These differences can be related to the oxygen content of the habitat of each species.

Whitney, R. J. (1939). "The thermal resistance of mayfly nymphs from ponds and streams." J. Exp. Biol. 16: 374–85.

Nymphs from slow or still waters have a greater resistance towards high temperatures than comparable nymphs from swift waters. This is correlated with the more extreme conditions of temperatures which are known to exist in slow and still waters. Differences of size or of efficiency in uptake of water-dissolved oxygen may account for the interspecific differences of thermal resistance. The author discusses the bearing of the results on the ecological distribution of the mayfly nymphs.

(*c*) Land

Harris, T. M. (1939). "Notes on a fencing experiment." J. Ecol. 27: 383.

The effect of sheep grazing on two types of vegetation widespread in North Wales was shown by the marked changes which were found after sheep had been excluded for two years. The protected quadrats had both a relatively greater luxuriance and an increase in edible species.

Smith, T. (1930–8). "The birds of Staffordshire." Originally issued as Appendices 1–9, Trans. N. Staffs. Fld Cl., Vol. 64 (1929–30) to Vol. 72 (1937–38). Reissued as one volume, 287 pp.

Contains many notes and records under species headings, with some data on changing status in various species. The introduction gives a general topographical description, a short discussion on migration routes in the county and a bibliography of works on Staffordshire ornithology.

Almond, W. E., Nicholson, J. B. & Robinson, M. G. (1939). "The birds of the Tees Valley." Trans. North. Nat. Un. 1: 229–51.

The Tees Valley runs down from the Pennines, mostly forming the boundary between Durham and Yorkshire, and providing wild moor and hill-stream habitats in the upper parts, and lowland agricultural and woodland ones below, and river. There is a full list of birds, with the usual type of general notes upon their distribution and status, but not very much detail about the habitat limits.

Morley, A. (1939). "The rising and roosting of a pair of resident starlings in winter and early spring." Brit. Birds, 33: 39–43.

Resident starlings increased their day length of activity equally with winter-roosting birds until 10 February. After that they increased it much more quickly in comparison, suggesting that onset of breeding condition is earlier in resident birds.

Thompson, H. W. (1939). "Agricultural entomology in Yorkshire." Ann. Appl. Biol. 26: 834–7.

A general account with special reference to the geological formations.

Dicker, G. H. L. (1939). "Insects associated with cultivated forms of *Rubus*." Trans. Soc. Brit. Ent. 6: 115–36.

Brief notes are given for the 132 species of insects observed to breed on, or to be associated with, cultivated forms of *Rubus*. Those of economic importance are described in more detail. Nine species of mites are also mentioned.

Niblett, B. (1939). "British gall-causing Cynipidae. II." Entomologist, 72: 157–60.

Records of gall-wasps bred from named host-plants.

Hertz, M. (1939). "New experiments on colour vision in bees." J. Exp. Biol. 16: 1–8.

In daylight a surface which reflects a fair proportion of ultra-violet, as well as the visible spectrum, is neutral or white to the bee. If the percentage of reflexion is less than one-third of the percentage of reflexion of visible light it appears coloured. Three types of European flowers are known: those which appear (1) orange-yellow for bee and man, (2) blue-violet for bee and man, (3) blue-green for the bee, but white, pink, light purple, bluish or yellowish for man. Ultra-violet is never present in such a way as to make flowers which are brilliantly white to man appear equally white to the bee.

Aubrook, E. W. (1939). "A contribution to the biology and distribution in Great Britain of *Boreus hyemalis* (L.) (Mecopt., Boreidae)." J. Soc. Brit. Ent. 2: 13–21.

Describes the process of copulation, the breeding of the Braconid parasite *Dyscoletes lancifer*, and the occurrence of partially grown larvae in summer. A map of the distribution in the British Isles is given, there are no records from Ireland or from the mid- and south-western counties of England.

Fletcher, T. Bainbrigge (1939). "Notes on Orthoptera in Gloucestershire." Ent. Rec. 51: 87–9.

Notes on distribution and relative abundance.

Burr, M. (1939). "Modern work on earwigs." Sci. Progr. Twent. Cent. 34: 20–30.

A short review of the distribution of the Dermaptera including also discussions of sense organs, maternal care, and ability of common earwig to fly.

Hassan, A. I. (1939). "The biology of some British Delphacidae (Homopt.) and their parasites with special reference to the Strepsiptera." Trans. R. Ent. Soc. Lond. 89: 345–84.

Describes the life histories of nine species of Delphacidae and gives a key for the identification of the nymphs. Discusses parasitic fungi, mites, Mymaridae and Dryinidae and gives the life history of the Stylopid parasite, *Elenchus tenuicornis*.

Marriner, T. F. (1939). "Coleoptera of Easton." Ent. Rec. 51: 121–7.

Useful distribution records with some ecological notes from north-east Cumberland. For Lepidoptera, see pp. 139–43; for Hemiptera, see pp. 160–1.

Ashe, G. H. (1939). "A note on *Scymnus minimus* Rossi (Col., Coccinellidae)." Ent. Mon. Mag. 75: 250.

This uncommon beetle was plentiful in webs spun by a red mite on gorse branches, Hartlebury Common, Kidderminster, September 1939.

Andrews, H. W. (1939). "Diptera bred from a wasps' nest." Ent. Rec. 51: 172.

A nest taken from a hollow willow at Norwood, S.E., produced *Scatopse fuscipes* (Bibionidae), *Tephrochlamys tarsalis* (Helomyzidae), and *Fannia lineata* (Anthomyiidae) in some numbers, also single specimens of *Hydrotaea dentipes* and *Acanthiptera inanis* (Anthomyiidae).

Grensted, L. W. (1939). "Diptera on the summit of Snowdon, Carnarvonshire." Ent. Mon. Mag. 75: 234–5.

Diptera, practically all Empididae (*Hilara chorica*), were swarming round the cairn and peak (3560 ft.) on a very hot, still day in August.

Kimmins, D. E. (1939). "Empididae (Dipt.) and the flowers of *Orchis elodes* Godfery." J. Soc. Brit. Ent. 2: 37–8.

Many of the flowers of this orchid observed at Leith Hill, Surrey, had small flies (chiefly *Empis praevia*) adhering by their wings to the sticky stigma. The flies so trapped were too small to be of service in pollination. Similar observations by others are also noted.

Cameron, E. (**1939**). "The holly leaf-miner (*Phytomyza ilicis*, Curt.) and its parasites." Bull. Ent. Res. 30: 173–208.

A general account of the systematics, synonymy, distribution, host relationship and biology followed by an account of the biology of six of the nine parasites, eight Chalcidoidea and one Braconid. Morphological details of the parasitic larvae are given. Egg, larval, prepupal and pupal stages serve to distinguish the parasites.

Barnes, H. F. (**1939**). "The Chrysanthemum midge." J.R. Hort. Soc. 64: 503–6.

This species has usually been recorded as *Diarthronomyia hypogaea*, but its true identity has not yet been decided. The larvae live in the tissues of the plant, causing cone-shaped galls.

Miles, H. W. (**1939**). "Wireworms and the breaking up of grass land." J. Minist. Agric. 46: 480–8.

Life history, effect of ploughing and cultivation, habits in relation to ploughing grass land, etc.

Graham, J. F. (**1939**). "The external features of the early stages of *Spathiophora hydromyzina* (Fall.) (Dipt., Cordyluridae)." Proc. R. Ent. Soc. Lond. B, 8: 157–62.

This fly, related to the yellow dungfly, amongst the higher Diptera, is the only successful colonist of the sewage bacteria beds; it preys upon the Chironomidae and Psychodidae which breed there. Features in the respiration and buoyancy maintenance of the larva are mentioned as possibly contributing to a successful life in this environment.

Colquhoun, M. K. (**1939**). "Flight and abundance of the winter moth." Entomologist, 72: 209–12.

The time of appearance of male winter moths is given, together with estimates of their abundance in flight. The abundance of settled moths was measured; while both sexes reached a maximum number at the highest temperature and humidity peak, there was throughout the period of sampling a continuous rise in the male to female ratio. There is some evidence to show that the behaviour pattern of the male undergoes modification simultaneously with a fall in temperature and consequent decrease in the number of emerging females.

Wigglesworth, V. B. (**1939**). "'Visual adaptation' among Lepidoptera: observations and experiments by F. Süffert." Proc. R. Ent. Soc. Lond. A, 14: 111–12.

A review of Prof. Süffert's views on cryptic coloration in larvae and pupae. Two main types of countershading are recognized. In the first type there is a single system: the body is darkest on the side where the light comes from and palest in the most heavily shaded regions, so that a single uniformly illuminated and therefore apparently flat surface is produced. In the second type a longitudinal pale line or "line of contrast" separates two regions which are countershaded independently, so that when illuminated in the normal manner two apparently flat surfaces of different tones, separated by a pale line, are produced.

Hull, J. E. (**1939**). "On the banks of Allen Water: in quest of subterranean spiders." Vasculum, 25: 112–16.

Five species (*Diplocentria blanda, D. saxetorum, Maro falconerii, M. minutus, M. persimilis*) may be found on the buried surface of firmly embedded stones, previously assumed to be inaccessible to spiders.

Wilson, G. Fox (**1939**). "Contributions from the Wisley Laboratory. LXXXVII. *Amaryllis* pests." J. R. Hort. Soc. 64: 318–26.

An account of the biology of the bulb-scale mite, *Tarsonemus laticeps*, which is concerned in the reddening of the leaves and flower stems of *Amaryllis* bulbs.

Gunn, D. L. (**1937**). "The humidity reactions of the wood-louse, *Porcellio scaber* (Latreille)." J. Exp. Biol. 14: 178–86.

A study of the reactions of this species to humidity show that it is very active in dry air and almost motionless in nearly saturated air. The humidity receptors evidently do not lie on the abdomen or the head region.

Cole, H. A. & Jones, E. W. Knight (1939). "Some observations and experiments on the setting behaviour of the larvae of *Ostrea edulis*." J. Cons. Int. Explor. Mer, 14: 86–105.

The behaviour at the important stage of attachment and metamorphosis is discussed. Details are given of selection of position, and the ability to delay attachment has considerable survival value.

Reynoldson, T. B. (1939). "On the life-history and ecology of *Lumbricillus lineatus* Mull. (Oligochaeta)." Ann. Appl. Biol. 26: 782–99.

This worm shows a wide range and tolerance of diverse chemical conditions. A complete account of the life history with special reference to hatching is given. A Ciliate (Anoplophryinae) was frequently present in the foregut and a *Monocystis* invariably occurred in the segments containing the testis lobes. Eggs were sometimes destroyed by a Ciliate of the genus *Glaucoma*. Bacterial beds form an environment for this worm which includes all the main features of its natural habits.

Powell, A. K. (1939). "Investigations upon the pea strain of *Heterodera schachtii* Schmidt and its role in the causation of pea sickness." Ann. Appl. Biol. 26: 572–84.

Both the Nematode *H. schachtii* and the fungus *Aphanomyces euteiches* can singly produce a pathological condition of the host in the absence of any other pathogenic factor, but there are indications that *H. schachtii* is the primary cause of pea sickness.

(*d*) Small islands

Warwick, T. (1939). "Animal life on Mingulay, Outer Hebrides." Scot Nat. 127.

A list is given of insects and land molluscs taken on Mingulay during early April 1938. Several specimens of the land planarian *Rhynchodemus terrestris* occurred under the stones of ruined crofts. Rabbits, and field mice (*Apodemus hebridensis*) which occasionally enter the inhabited house, were common, but brown rats and house mice were apparently absent.

Miller, E. (1939). "Coast birds in June and July." Vasculum, 25: 21–2.

Brief notes made from 1911 to 1914 on the Farne Islands, on sheld-duck and various waders.

Waterston, A. R. (1939). "Insects from Colonsay, South Ebudes." Scot. Nat. 128–31.

A list is given of species of Orthoptera, Odonata, Trichoptera, Lepidoptera, Coleoptera, Hymenoptera and Diptera collected on Colonsay during the first half of July 1938. It includes *Hister unicolor* and *Melolontha hippocastani*, which are here recorded from the Western Isles for the first time although museum specimens of the former collected from the west of Scotland exist; *Cyphon ochraceus* and *Colletea floralis*, which occurs on or near the coast in south and west Ireland and western Scotland, and which was abundant on Pabbay in June 1936.

Harrison, J. W. Heslop (1939). "*Bombus hortorum* L. (Hym.) at sycamore flowers on the Isle of Coll." Ent. Mon. Mag. 75: 252.

Over 80 queens of this humble bee were observed. This is remarkable as at Arinagour *Bombus smithianus* outnumbers *B. hortorum*, and a little to the south-west *B. ruderarius* exceeds both in numbers. On both Tiree and Coll *B. smithianus* is by far the commonest and most widely distributed bee.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

Praeger, R. L. (1939). "The relations of the flora and fauna of Ireland to those of other countries." Proc. Linn. Soc. Lond. 1938–9: 192–213.

A preliminary discussion of the effects which separation and climatic differences have had on the flora and fauna of Ireland when compared with those of Britain and the European mainland.

Gilmour, J. S. L. & Gregor, J. W. (1939). "Demes: a suggested new terminology." Nature, Lond. 144: 333.

Defines and gives examples of the use of the following terms: *Deme*: any assemblage of taxonomically closely related individuals. *Gamodeme*: a deme forming a more or less isolated local interbreeding community. *Topodeme*: a deme occupying any specified geographical area. *Ecodeme*: a deme occupying any specified ecological habitat.

Grimshaw, P. H. (1939). "Classified index of entomological contributions to the *Scottish Naturalist* from its commencement in 1871 to the end of 1938." Scot. Nat.: 105–20, 137–85.

Separate alphabetical author reference lists under each taxonomic group.

van Emden, F. (1939–40). "Larvae of British beetles. I. A key to the genera and most of the species of British Cerambycid larvae." Ent. Mon. Mag. 75: 257–73; 76: 7–13.

The first of a projected series of keys for the identification of the larvae of British beetles.

Johnson, C. G. (1939). "Taxonomic characters, variability, and relative growth in *Cimex lectularius* L. and *C. columbarius* Jenyns (Heteropt. Cimicidae)." Trans. R. Ent. Soc. Lond. 89: 543–68.

The pigeon-bug resembles the bed-bug so closely that identification has been very difficult and many workers have thought that they are the same species. It is shown that the species produce fertile hybrids from the two reciprocal crosses and *C. columbarius* is, therefore, regarded as a subspecies of *C. lectularius*. The morphological differences between the two are discussed statistically.

Edwards, F. W., Oldroyd, H. & Smart, J. (1939). "British blood-sucking flies." Pp. viii+156, 45 plates. London: British Museum (Nat. Hist.). Price 15*s*.

The aim of this work is to provide in the simplest manner information of interest to non-specialists; technical terms are so far as possible avoided, and no attempt has been made to give full descriptions of the insects, while in the Nematocera, the males (which do not suck blood) have been omitted from consideration. There is, however, a brief summary of facts regarding the habits, life history, and distribution in Britain of every blood-sucking fly known to occur within the British Isles.

Scott, Eunice I. (1939). "An account of the developmental stages of some aphidophagous Syrphidae (Dipt.) and their parasites (Hymenopt.)." Ann. Appl. Biol. 26: 509–32.

Chiefly concerned with descriptions of and a key to Syrphid pupae, but including notes on the eggs. Larvae may be differentiated by the nature of the posterior respiratory trunk which is unaltered in the pupal stage. Notes on Ichneumonid, Chalcidoid and Proctotrupoid parasites, including descriptions of the mouth-parts of mature larvae of certain Ichneumonid parasites.

Edwards, F. W. (1939). "Additions to the list of British crane-flies." Ent. Mon. Mag. 75: 241–9.

Adds 11 species to the British list and includes a key to the species of *Nephrotoma*.

Richards, O. W. (1939). "The British Bethylidae (*s.l.*) (Hymenoptera)." Trans. R. Ent. Soc. Lond. 89: 185–344.

An important systematic paper, well-provided with keys, illustrations and distribution records. Includes the Dryinidae, parasites of Homoptera; and Bethylidae (*s.s.*), somewhat intermediate in habits between fossorial Hymenoptera and true parasites. Gives a revised check-list of the British species.

Hallett, H. M. (1939). "Guide to the collection of British Aculeate Hymenoptera." Published by the National Museum of Wales and by the Press Board of the University of Wales. Cardiff. Pp. 28. Price 4*d*.

The collection numbers about 7000 specimens, but contains no Bethyloidea, although 90% of the remaining British Aculeates are represented. It is rich in specimens from Burton-on-Trent, West Suffolk, Glamorgan and other Welsh border counties. Only the more interesting species are mentioned by name, for some of these ecological notes are given.

Bagnall, R. S. (1939). "Notes on British Collembola." Ent. Mon. Mag. 75: 21–8, 56–9; 91–102; 188–200.

A systematic paper which adds a number of species new to the British fauna, and includes some ecological notes.

Bristowe, W. S. (1939). "The comity of spiders." London: Ray Society Publ. 8vo. Vol. 1. Pp. x+228, 15 figs., 19 plates. Price 25*s*.

Includes lists of the 556 British species, the counties in which they occur and their distribution abroad; a discussion of distribution by environments (plant and soil preferences; sandhills; marshes; mountains; caves; mines and cellars; houses, towns, sewage works; various invertebrate and vertebrate nests); dispersal (land bridges, transportation by man, dispersal by air, island faunas); and an account of the spider population, with a calculation of the distances travelled by males in their search for females.

Rolfe, S. W. (1939). "Notes on Diplopoda. VI. The recognition of some millipedes of economic importance—III." J. S.-E. Agric. Coll. Wye, 44: 180–2.

Figures of the vulvae of Polydesmidae and Strongylosomidae. Those of the Iulidae were illustrated in 1938, ibid. 42: 214–15.

Birks, S. G. Brade- (1939). "Notes on Myriapoda. XXXVI. Sources for description and illustration of the British fauna." J. S.-E. Agric. Coll. Wye, 44: 156–79.

A most valuable check-list of the British species with references to descriptions and illustrations of them.

Gurney, R. (1939). "Bibliography of the larvae of Decapod Crustacea." London: Ray Society Publ. vii+123 pp.

Alphabetical list of authors with cross-reference from classified list of species.

Garstang, W. (1939). "Nomenclature of Nudibranch Mollusca." Nature, Lond. 144: 481.

A spirited criticism of **Iredale & O'Donoghue** (1923), Proc. Malac. Soc. 15: 195–233, deploring the sinking of generally accepted names.

3. Parasites

Robertson, D. (1939). "Helminths from hill sheep." Scot. J. Agric. 22: 231–5.

Twelve species of nematodes and two species of cestodes were recovered from hill lambs, and thirteen nematodes, two cestodes and one trematode from hill ewes. Heavy infestations of *Ostertagia* sp. and *Bunostomum trigonocephalum* were found in three out of the eleven lambs examined and of *Trichostrongylus vitrinus* in two of the twenty ewes. All the lambs were infested with *Haemonchus contortus*, *Ostertagia circumcincta* and *Nematodirus* sp. and all the ewes with *Bunostomum trigonocephalum*.

O'Mahony, E. (1939). "Notes on Irish Siphonaptera. I." Ent. Mon. Mag. 75: 253–4.

Refers to three species new to Ireland, a new host record and the results of some breeding experiments carried out with bird fleas.

Moon, H. J. (1939). "*Ornithomyia lagopodis* Sharp (Dipt.) taken from a sandpiper." J. Soc. Brit. Ent. 2: 38.

Apparently the first record from this host.

Narayanan, E. S. (1939). "'Auto-parasitism' by *Nemeritis canescens* (Grav.) (Ichneumonidae)." Nature, Lond. 144: 207.

Nemeritis canescens is a parasitoid of *Ephestia kühniella*. Oviposition into pupae of the same species is observed and third instar larvae found in the abdomen of the adult insect.

Friend, G. F. (1939). "Gill parasites of brown trout in Scotland." Scot. Nat.: 123–6.

Five females of the Copepod gill parasite *Salmincola gordoni* were taken on two small brown trout (*Salmo trutta*) from the river Devon, Perthshire, in May 1938, and eight mature females of the same species occurred on five trout from Loch Lyon, Perthshire, in May 1939. The parasites were attached to the wall of the gill chamber or to the gill cover, never to the gill filaments. Previous records of *Achtheres percarum* on trout in Scotland in 1877, 1894, and 1913 probably refer to this species, but still another species of *Salmincola* may be indicated. Parasitic Copepods appear to be uncommon on trout in Scotland and have not been recorded on grayling there. The adult female is briefly described. Eight specimens of the fluke *Discocotyle saggitata* also occurred on one of the trout from the river Devon. This species, which has not previously been recorded from Scotland, is common near Edinburgh, in Peebleshire, on Barra and in Glen Devon.

4. Food and food habits

Swynnerton, G. H. & Worthington, E. B. (1939). "Brown-trout growth in the Lake District: a study of the conditions in 'acid' lakes and tarns." Salm. Trout Mag. No. 97: 337–55.

A study of the growth of brown trout (determined from scale readings) in three lakes and three tarns. It is tentatively concluded that the growth rate depends primarily on the relation between the number of trout present and the amount of food available and that these factors are related to the general "productivity" of the waters. This, in turn, depends on their geological history.

Moon, H. P. (1939). "Relationship between aquatic insect larvae and the food of fresh water fish." J. Soc. Brit. Ent. 2: 13.

The stomachs of a stone loach (*Nemachilus barbatula*) and of a salmon parr (*Salmo salar*) contained numerous Orthocladian midge larvae whose food consisted chiefly of diatoms.

Richards, O. W. & Hamm, A. H. (1939). "The biology of the British Pompilidae (Hymenoptera)." Trans. Soc. Brit. Ent. 6: 51–114.

A very important paper on a group of wasps in which the female typically catches and paralyses a spider and then constructs a burrow for its reception, subsequently laying an egg upon it. Comprises a discussion of general biological questions, followed by details concerning the biology and spider prey of 39 species and a lengthy list of references.

Hooper, C. H. (1939). "Hive bees in relation to commercial fruit production." J. S.-E. Agric. Coll. Wye, 44: 103–8.

Includes references and sources of further information relating to insects in relation to the pollination of fruit and clover as well as self-fruitfulness, self-sterility and incompatibility of fruit trees.

Jary, S. G. & Austin, M. D. (1939). "Investigations on insect pests of *Brassica* seed crops in Romney Marsh." J. S.-E. Agric. Coll. Wye, 44: 73–83.

Deals with the pollen-feeding beetle *Meligethes aeneus*; includes notes on its life cycle, and methods of control.

Dicker, G. H. L. (1939). "The morphology and biology of the bramble shoot-webber, *Notocelia uddmanniana* L. (Tortricidae)," Ann. Appl. Biol. 26: 710–38.

Includes a detailed study of the biology of this Tortricid. Loganberry and phenomenal berry suffer severely from attacks, but raspberry and the cultivated blackberries are far less attractive. Numerous other *Rubus* species provide an adequate food supply. Wild blackberry is a favourite host plant. An Ichneumonid, *Omorgus mutabilis*, parasitized 35–50% of the larvae in the East Malling district. Other parasites found were an *Apanteles* and a Tachinid fly, *Nemorilla notabilis*.

Dicker, G. H. L. (1939). "The bramble shoot-webber (*Notocelia uddmanniana* L.)." Rep. E. Malling Res. Sta. 1938, 191–8.

A preliminary report on the life history and control of a species of Tortricid moth found only on plants of the genus *Rubus*. Includes a graph to show the emergence of the caterpillars from hibernation in 1937 and 1938.

Huggins, H. C. (1939). "A few notes on *Platyptilia tesseradactylus*." Entomologist, 72: 177–8.

The larva of this plume-moth feeds in the spring on the flower shoot of *Antennaria dioica* and probably leaves the stem when full-fed to pupate amongst rubbish. The moth occurs in Ireland and has a wide central European and Scandinavian distribution, but it has not been discovered in Great Britain although the food plant is widely distributed there.

Haines, F. H. (1939). "*Aglais urticae* L. (Lep., Nymphalidae) taken by blackbird." Ent. Mon. Mag. 75: 202. See also **W. Parkinson Curtis,** 1939, J. Soc. Brit. Ent. 2: 38, 39 for further references to Lepidoptera taken by birds.

Harrison, J. W. Heslop (1939). "*Depressaria nervosa* Haw. and *D. heracleana* De Geer (Lep., Oecophoridae) in the Hebrides." Ent. Mon. Mag. 75: 253.

Notes on the distribution of these moths and of their food plants.

MacGill, E. I. (1939). "A Gamasid mite (*Typhlodromus thripsi* n.sp.), a predator of *Thrips tabaci* Lind." Ann. Appl. Biol. 26: 309–17.

Life history and description of this predacious mite.

Cole, H. A. (1939). "Further experiments in the breeding of oysters (*Ostrea edulis*) in tanks." Minist. Agric. Fish., Fish. Invest. Ser. 2, 16, No. 4: 1–47. (London: H.M. Stationery Office. Price 2*s*.)

Confirms the commercial possibilities for British oyster growers of tank culture and planting of settled spat. High nannoplankton density ensures good growth, settlement and survival. Temperature fluctuations around a mean of 16–17° C. are likely to produce spawning in ripe females.

Wild, S. V. & Lawson, A. K. (1937). "Enemies of the land and freshwater Mollusca of the British Isles." J. Conch. 20: 351–61.

For each snail is given a list of natural predators, together with literature reference.

Cameron, A. E. (1939). "The control of potato slugs." J. Minist. Agric. 46: 454–62.

The injurious species, the life history of the grey field slug, slugs and their environment, habits and damage, as well as the course of slug infestation and control, especially by "meta".

Johnson, L. R. (1939). "Further observations on *Anguillulina dipsaci* in rhubarb." Ann. Appl. Biol. 26: 739–49.

The rhubarb strain of this roundworm is capable of producing persistent infection in oats, pea and chickweed and temporary infection in cabbage and mangold.

5. Population studies

Jackson, C. H. N. (1939). "The analysis of an animal population." J. Anim. Ecol. 8: 238–46.

An estimate of the total numbers in any given animal population is made by selecting a definite area, catching, marking, and releasing a random sample of individuals, then later catching another random sample evenly distributed over the same area. Subject to certain conditions, the number of marked individuals recaptured should bear the same relation to the total animals in the second catch as the number of individuals marked in the first catch bears to the total population. Losses through death and emigration, and increases through birth and immigration are computed. The method is worked out by a series of mathematical formulae. Though developed for estimating tsetse fly populations in East Africa, the method is considered to have a much wider application.

Diver, C. (1938). "The distribution of natural populations." Proc. Zool. Soc. Lond. C, 108: 61–2.

No populations are entirely continuous over large areas. Whether natural selection is operative or not, this is obviously conducive to the formation of new races; it is suggestive that race-formation seems to be more pronounced among those organisms, e.g. mammals and birds, which, though the most capable of voluntary movements, are the least likely to be affected by involuntary dispersal.

Thompson, W. R. (1939). "Biological control and the theories of the interactions of populations." Parasitology, 31: 299–388.

A critical survey of the application of mathematics to population studies, especially in the field of economic entomology. The author's thesis is that the mathematical theory of populations due to Volterra is not at present in a form applicable to the interactions of living organisms and cannot replace direct observation and experiment as a basis for practical operations in economic biology.

Greenwell, J. (1939). "Notes from the Bishop Auckland district." Vasculum, 25: 106.

Foxes are now numerous and are shot and trapped in considerable numbers. Stoats are now very common in the Dale, but weasels comparatively rare; 10 years ago the position was reversed. Badgers are plentiful. Red squirrels are again plentiful after some years of scarcity, but the grey squirrel has not yet reached the district. Includes a few notes on greater spotted woodpeckers, kestrels and merlins.

Brambell, F. W. R. & Hall, K. (1939). "Reproduction of the field vole (*Microtus agrestis hirtus* Bellamy)." Proc. Zool. Soc. Lond. A, 109: 133–8.

Details given of sex ratio, growth, breeding season, fertility, oestrous cycle.

H[arrison], J. W. H[eslop] (1939). "The rabbits on the Isle of Coll." Vasculum, 25: 102.

Records extraordinary numbers, also weird-looking patterns and colours (black, ginger, white; others bluish-black and white, etc.). The common wild type possibly formed the majority of the population, but the shiny, jet-black examples attracted attention, 4000 couples of coloured ones have recently been taken for their skins.

Harry, E. L. (1939). "Some aspects of the sheep industry in Wales." Welsh J. Agric. 15: 129–50.

Includes figures of sheep in Wales in 26 years from 1867 to 1938 and the changes in county populations since 1893.

Oakes, C. & Battersby, E. (1939). "The birds of East Lancashire." 89 pp., 1 map, and 4 photos. Burnley Express Printing Co., Ltd., Burnley. Price 6*s*.

Comprises a review of the status of each bird on the county list arranged in systematic order. Many interesting changes in status are recorded, and notes on various biological aspects are added in some cases. Thus there are remarks on the roosting habits of rooks, on the winter distribution of snow buntings, and on the migrations and routes of lesser black-backed gulls. There are also a number of notes on Passerine migrations.

Heycock, C. W. (1939). "Changes in birds in the Winchester district, 1932–38." Bird Notes News, 18: 111–15.

Contains an account of the effect on birds of creating a reserve from two and a half acres of water meadows, which was allowed to go wild. Unharvested fields were soon occupied by short-tailed field voles (*Microtus*), which reached a peak in the winter of 1937–8. Barn owls and kestrels were the chief predators.

Edwards, V. C. Wynne- (1939). "Intermittent breeding of the fulmar (*Fulmarus glacialis* (L.)), with some general observations on non-breeding in sea-birds." Proc. Zool. Soc. Lond. A, 109: 127–32.

Wearing down of the claws is shown to be correlated with the amount of breeding, as evidenced by the number of resorbed follicles in the ovary. A sample of non-breeding birds showed that they belonged to mixed age groups.

Southern, H. N. (1939). "The status and problem of the bridled guillemot." Proc. Zool. Soc. Lond. A, 109: 31–41.

Summarizes the distribution of a bridled mutant, showing a gradient in dimorph ratio from less than 1% in France and southern England to more than 50% in the high north. The gradient is a stepped one.

Lack, D. (1939). "Further changes in the Breckland avifauna caused by afforestation." J. Anim. Ecol. 8: 277–85.

The distribution of birds on the open "brecks", heaths, and pine plantations from 4 to 15 years old is presented as the percentage which each bird forms of the total number of birds seen in walking counts, in the breeding season and in mid-winter. Counts, not on a percentage basis, are also given for mid-summer birds. The rapid and steady changes in bird population with the increasing height of the trees provide an interesting example of ornithological succession. The arrivals of colonizing species which can be analysed seem correlated mostly with song posts and nesting sites.

Venables, L. S. V. (1939). "Bird distribution on the South Downs, and a comparison with that of Surrey Greensand heaths." J. Anim. Ecol 8: 227–37.

The distribution of birds (numbers of pairs seen per mile) in the breeding season, the end of April and early May, is correlated with types of vegetation on the Chalk and Greensand. Eight types are recognized on the chalk, the main ones being grassland, thick and sparse, and scrub, deciduous and evergreen, closed and open. A table lists 42 species for the eight chalk types and two Greensand types, pine scrub and gorse scrub. It was rare for a bush-nester or bush-singer to breed where there is not a great number of bushes (i.e. scrub) or a ground-nester and air-singer where there is not a big expanse of grass. Most attention is devoted to the chalk, as the Greensand types of vegetation and bird distribution have been described in an earlier paper by the same author (J. Anim. Ecol. (1937), 6: 73–85).

Chapman, W. M. M. (1939). "The bird population of an Oxfordshire farm." J. Anim. Ecol. 8: 286–99.

Observations made in 1931–5 on the same farm of about 300 acres, the eastern half of which was covered in 1926–31 and reported on by **W. B. Alexander** in his paper under the same title in J. Anim. Ecol. (1932) 1: 58–64, and partly supersedes the earlier paper. The counts were made more frequently and regularly than the earlier ones, and covered also the western half of the farm. Pasture, arable land, hedges and small copses are included. The results are presented mainly in five tables showing for each species the number of times recorded out of the number of counts, and the average number of birds per 100 acres, for winter populations with a comparison of pasture and arable, and for summer populations; there is also a comparison of summer and winter. The winter population on pasture varied from 3·6 to 5 birds per acre, and on arable from 3·7 to 7, and was most constant for birds dependent on the hedges. The summer population was more constant, and roughly half of the winter population, as it does not have the flocks characteristic of the latter.

Brown, R. H. (1939). "Notes on the lapwing and curlew breeding populations of a Cumberland farm." Brit. Birds, 33: 12–15.

Gives counts for both species over two years on 650 acres: also discusses habitat preferences, distribution, mortality.

Thompson, W. D'Arcy (1939). "Fishery statistics." Nature, Lond. 144: 445.

By reducing monthly quantities to percentages of the annual figure and comparing the periodicity of one year with another, the discrepancies can be shown to yield a nearly regular fluctuation, and tell how the phase of the periodic fluctuation was accelerated in one year and retarded in another.

Rae, B. B. (1939). "Age and growth of lemon soles in Scottish waters." Fisheries, Scotland, Sci. Invest., 1939, No. 1: 1–39. (Edinburgh: H.M. Stationery Office. Price 1*s.* 6*d.*)

Analysis of lemon sole catches of the research vessel *Explorer* during 1922–36. A useful discussion of validity of scale reading, with some good new material, including a survey of the scales from different parts of a fish. Lateral line scales 75th–95th from the head give the most accurate readings. Greatest commercial toll is taken of each brood in the fourth to seventh years of life. The variation between good and poor broods does not exceed 3 : 1 (except locally). Because of this small ratio and also for the following reasons the fishery is able to yield uniformly good catches. The large number of broods (9–13) in the commercial catch; the long and favourable spawning period and its wide-spread nature; the relatively small number of immatures (especially females) destroyed by the trawl. Six growth zones are distinguished, good in the Firth of Forth, less good the farther north. Sizes calculated from scales are low, from otoliths high compared with observed sizes.

Gerrish, C. S. (1939). "A trout-marking experiment: further notes from the Gade investigations." Salmon Trout Mag. No. 96: 224–32.

Brown trout in the River Gade were measured, scales taken for examination, marked and released and the data compared with those obtained when the fish were recaptured between 4 and 17 months later. In a few cases the fish had stopped growing for periods up to 1 year, and hence the age recorded by the scale was inaccurate. Some of these fish later grew normally and their scales grew proportionately. Few fish spawned annually and 1–2-year-old fish when transplanted to another part of the river stayed in their new home, while older fish generally returned to their old habitat.

Neill, R. M. (1939). "Reproductive cycle in *Salmo salar* Linn." Nature, Lond. 144: 332.

Examination of the ovaries of a female salmon, whose scales carried a spawning mark for the winter preceding the capture. The ovary contained an apparently full complement of old ova in various stages of resorption and infiltrating new ova.

Bullough, W. S. (1939). "A study of the reproductive cycle of the minnow in relation to the environment." Proc. Zool. Soc. Lond. A, 109: 79–102.

The effect of environmental factors on reproductive function is considered in the light of recent work on photoperiodicity. Various combinations of light and temperature were used. Both sexes showed stimulation of early gonad development (oogonia and spermatogonia) by temperature raising, but final stages needed extra light as well as the rise in temperature.

Kemp, S. (1938). "Oceanography and the fluctuations in the abundance of marine animals." Rep. Brit. Ass. Cambridge: 85–101.

An account of recent work on marine populations, with special reference to the research in Britain on the relation between the population of fish and the phyto- and zooplankton. Long-term fluctuations in oceanic populations may be brought about in different ways. In the English Channel changes in population can be traced to a deficiency in phosphate and in more northerly regions they are due to an increase in sea-temperature. The main features of recent detailed research on the hydrography of the North Atlantic are discussed.

Garstang, W. (1937). "On the size-changes of diatoms and their oceanographic significance." J. Mar. Biol. Ass. U.K. 22: 83–96.

Wimpenny's theory of selection (1936, *ibid.* 21: 29–60) to account for a supposed relation between rising temperature and increase in average width of populations of *Rhizolenia styliformis* is criticized. His figures are taken to show the significance of population curves in interpreting North Sea water movements and mixtures.

Flemming, R. H. (1939). "The control of diatom populations by grazing." J. Cons. Int. Explor. Mer, 14: 210–27.

In a mathematical study of the influence of filter feeders on phytoplankton populations, an equation is developed for computing the total production. It is shown that dense phyto- and zooplankton are unlikely to occur together.

Tattersall, W. M. (1938). "The seasonal occurrence of Mysids off Plymouth." J. Mar. Biol. Ass. U.K. 23: 34–56.

Two maxima occurred in numbers taken just off the sea bottom: (1) in July and August caused by the planktonic habit of *Leptomysis gracilis* in its breeding season, (2) in December and January caused by immature forms possibly concentrated by temperature in the bottom layers.

Harrison, J. W. Heslop (1939). "The present position of our local butterflies compared with that of 40 years ago." Vasculum, 25: 117–20.

Records of 32 species, some of which have now disappeared from the localities in which they were formerly found.

Michael, P. (1939). "Exceptional broods of *Eumenis semele* and *Maniola tithonus* in north-east Hants." Entomologist, 72: 294.

During the second week of August 1939 exceptionally large numbers of these butterflies were noted in the Aldershot (Hampshire) district, where they are usually plentiful in normal seasons. On 13 and 14 August they were in swarms, hundreds being in evidence in one small area comprising a few acres of heathland and rough hillsides.

Baines, J. M. (1939). "Abundance of *Maniola jurtina*." Entomologist, 72: 241.

On 30 July 1939 the meadow brown butterfly was to be seen in clouds in hayfields near Hastings.

Gordon, C. (1939). "A method for the direct study of natural selection." J. Exp. Biol. 16: 278–85.

A record of experiments on selection of mutants of *Drosophila melanogaster*. A balanced population containing 25% ebony mutants was released in Devon. By a system of trapping, followed by tests for heterozygosis, it was found that the frequency value of the genotype was very close to a value which could be deduced on the assumption that elimination of the recessive type took place before the completion of maturity.

Robertson, A. G. (1939). "The nocturnal activity of crane-flies (Tipulinae) as indicated by captures in a light trap at Rothamsted." J. Anim. Ecol. 8: 300–22.

Activity for 1933–6 is presented for seven species of Tipulinae. Ten other species were caught in very small numbers. By far the most abundant, 57·4% of the total, was *Tipula paludosa*. In general, males appear at the light in greater numbers than females. The distribution was from May to November, the peak occurring in September. The greatest activity is just after sunset, with a secondary maximum usually just after midnight, except for *T. paludosa* in which the secondary maximum is just before daylight. Activity is favoured by high minimum temperature and by a small range of temperature (difference between minimum and maximum), but is not correlated with maximum temperature. Optimum conditions are absence of moonlight and complete cloudiness, when the catch is eight or nine times as large as under the least favourable conditions. The effect of cloudiness is related to the higher minimum temperature.

Mellanby, K. (1939). "The physiology and activity of the bed-bug (*Cimex lectularius* L.) in a natural infestation." Parasitology, 31: 200–11.

A bed-bug population in an animal room inhabited by rats was investigated. Feeding and fertilization frequencies and activity rhythms were studied. By means of marking experiments a rough estimate of population size and maximum length of life under the given conditions was obtained. The latter was short in comparison with that found in a control laboratory population, suggesting that the bugs are killed by the rats while feeding.

James, H. C. (1939). "Further studies on the reproductive methods of certain species of Coccidae (Homoptera)." Trans. R. Ent. Soc. Lond. 89: 569–77.

Tabulates the reproductive records of 70 female *Orthezia insignis*, 66 *Pseudococcus nipae* and 37 *Saissetia nigra*.

Glasgow, J. P. (1939). "A population study of subterranean soil Collembola." J. Anim. Ecol. 8: 323–53.

Samples were taken from May 1936 to September 1939 in an 80 × 50 ft. space in a long-neglected meadow on heavy clay soil at Slough, and the animals separated by the Ladell flotation method, identified and counted. Four layers were sampled, 4·5, 4·5–9, 9–13·5 and 13·5–16 in. Figures were obtained on ignition loss, moisture and temperature of the soil. The four truly subterranean species, *Onychiurus armatus*, *O. ambulans*, *Tullbergia quadrispina*, and *T. krausbaueri*, were all aggregated. *O. armatus* is correlated with moisture under wet conditions, and *O. ambulans* under dry conditions. The vertical distribution of each species is different, and that of *O. ambulans* shows seasonal changes. Both species of *Onychiurus* show winter maxima. The highest density of Onychuridae corresponded to one animal to 8 c.c. of soil. As each species has widely differing properties, the reactions of one species are no guide to the reactions of the others. The census counts and a description of a simple soil sampler are given in an appendix.

Diver, Cyril (1939). "Aspects of the study of variation in snails." J. Conch. 21: 91–141.

General review of some of the problems of molluscan variation with particular reference to the British non-marine fauna, particularly "The behaviour and classification of variation", and "The structure and study of natural populations".

6. Migration, dispersal and introductions

Garvey, T. (1935). "The muskrat in Saorstát Éireann." J. Dep. Agric. Saorstát Éireann, 33: 189–95.

150 sq. miles were colonized between 1927 and 1933, starting apparently from one pair. 487 were trapped in the winter of 1933–4.

Glegg, W. E. (1939). "The occurrence of the white stork (*Ciconia c. ciconia*) in Essex." Essex Nat. 26: 133–6.

The white stork is a rare visitor to England, and had only been recorded three times in Essex, until one turned up at Tollesbury in August 1938. A photograph of it sitting on a brick chimney top is reproduced. Although it had been thought that this bird was a captive, or else one of those released in the Haslemere Educational Museum experiment in 1936, a radio enquiry revealed no escapes, while the individual was not ringed on the leg.

Huntsman, A. G. (1939). "Races and homing instinct; a further paper." Salm. Trout Mag. No. 96: 233–7.

A contribution to the controversy about the homing instinct of salmon, pointing out the weaknesses of the evidence for the return from a distance of salmon to the river in which they were reared.

Macan, T. T. (1939). "Notes on the migration of some aquatic insects." J. Soc. Brit. Ent. 2: 1–6.

Includes observations on Corixidae in flight and an account of the effect of cleaning upon the fauna of the basin of the fountain at King's College, Cambridge.

Grensted, L. W. (1939). "Colonisation of new areas by water-beetles." Ent. Mon. Mag. 75: 174–5.

A small canvas tank set up in an Oxford garden on a summer's evening and filled with tap water was populated 24 hr. later by over 100 water-beetles, the majority being *Helophorus brevipalpis*. The full record for a week is also given. See also **E. J. Pearce** (1939), Ent. Mon. Mag. 75: 208.

Walsh, G. B. (1939). "Extension of range of the water beetle, *Hygrobia tarda* Herbst. (Col., Hygrobiidae)." Ent. Mon. Mag. 75: 239.

Suggests that there has been an amelioration of climatic conditions in much at least of the north of England and that this may provide an explanation for the northward spread of this water-beetle.

Beare, T. Hudson- (1939). "*Cis bilamellatus* Fowler (Col.) in Sherwood Forest." Ent. Mon. Mag. 75: 279.

This beetle, discovered in West Wickham Wood in 1884, is steadily extending its range and has now reached Sherwood Forest. It is probably a native of the Australian region.

Marriner, T. F. (1939). "Movements of Coccinellidae." Ent. Rec. 51: 104–6.

Migration routes of the lady-bird *Adalia bipunctata* in central and northern England for 1925 are described and mapped. The routes avoid the Peak and gaps in the Pennines are utilized. It would appear that an early warm spring in France, leading to quick maturing and consequent overcrowding may be responsible for the migration movements which, when small, seem to be absorbed in the south of England. Over 60% of the migrants were females. *C. septempunctata*, *C.* 11-*punctata*, *C.* 10-*punctata* and *Mysia oblongogutta* sometimes mass together in swarms.

Ashe, G. H. (1939). "*Stenopelmus rufinasus* Gyll. (Col., Curculionidae)." Ent. Mon. Mag. 75: 249.

This weevil, added to the British List in 1921, is now probably widely spread in southern England. In August, 1939, a rough estimation suggested that the population of an approximately circular pond of 15 yd. diameter was at least half a million.

Morley, B. D. W. (1939). "The disappearance of *Formica pratensis* Retz and *Formica execta* Nyl. (Hym. Formic.) from Bournemouth." J. Soc. Brit. Ent. 2: 24.

An invasion of *Formica rufa* is considered responsible for the disappearance of these two ants, formerly common in the Bournemouth pine woods.

Dannreuther, T. (1939). "Migration Records, 1939." Entomologist, 72: 273–83.

The 1939 season was remarkable for immigration of the cabbage whites, which extended from the end of May to the end of August. We have no records from the Baltic region, such as we had in 1937, to fix the area of origin; and whereas in 1937 the main flights arrived along the north coast of Norfolk and were mainly of *Pieris brassicae*, in 1939 *Pieris rapae* sometimes predominated and appeared to come down the English Channel, landing anywhere from Kent to Devon, and there was a corresponding abundance in northern France. A northerly migration of *Vanessa cardui* across France in the spring producing an abundance of larvae in the north-west, and causing some damage to globe artichoke crops, suggested a mass emergence in August, but heavy rains appear to have wiped out that generation in Finistère. There were, however, sufficient spring immigrants here to bring the autumn butterflies well above the average, in marked contrast to *Vanessa atalanta*, which has been unusually scarce.

Bretherton, R. F. (1939). "Migratory Lepidoptera in the Oxford District." Ent. Mon. Mag. 75: 250–1.

The list of species is a short one and its character suggests that the district is not on a regular route for more than a few species and these the common ones. This is explained on geographical grounds.

Harrison, J. W. Heslop (1939). "Immigrant Lepidoptera in the Inner and Outer Hebrides during 1939." Ent. Mon. Mag. 75: 252.

Notes on the occurrence of three species of butterflies and two moths.

Campbell, J. L. (1939). "Migrant Lepidoptera in Canna." Scot. Nat. 239: 132–3.

Owing to the fine spring, the following species had occurred on Canna before the end of the first week in June: *Pieris napi, Vanessa cardui, V. atalanta, Plusia gamma,* and *Nymphalis io.* The latter may be resident and is more widely distributed in the west of Scotland than was supposed. *Pieris napi* was also observed on Sanday.

Eliot, N. (1939). "*Vanessa cardui*: a possible line of migration." Entomologist, 72: 201–6.

In mountain areas such as those traversed there will usually be a route, dependent upon the configuration of the ground, which a majority of a migrating swarm will follow "naturally" rather than "instinctively". The author believes that the bluff at the junction of the Arc and Isère Valleys is probably a key position on such a route.

Rowley, G. D. (1939). "*Vanessa cardui* and *Pieris brassicae* in S. Cornwall and N. Devon; Autumn, 1939." Entomologist, 72: 291–2.

Both butterflies were in very great abundance at St Austell. At Ilfracombe the large white was very common to the exclusion of other Pierids and about 30% of the larvae under observation were parasitized.

Blair, K. G. (1939). "Abnormal abundance of the larvae of *Pieris brassicae* L. (Lep.) in South Devon." Ent. Mon. Mag. 75: 256.

Cabbages, and particularly broccoli, in the Start area of South Devon appear to have suffered severely (September 1939) from the depredations of this species, both as a field crop and in the gardens, the plants being frequently reduced to a mere bunch of midribs. Not a single group of the yellow cocoons of *Apanteles glomeratus*, the usually abundant parasite of this species, was to be seen.

Tulloch, B. (1939). "Extraordinary abundance of larvae of *Pieris brassicae*." Entomologist, 72: 266.

The second brood of this butterfly was numerous, but nothing out of the ordinary, although the larvae produced all seemed to have come to maturity and never before, in any part of the world, has the author seen plants so completely stripped of foliage.

Taylor, J. E. Campbell- (1939). "Abnormal abundance of the larvae of *Pieris brassicae* L. (Lep.)." Ent. Mon. Mag. 75: 278.

In 1939 the larvae of this butterfly were very abundant along the south coast of Pembrokeshire. The Braconid parasite *Apanteles glomeratus* was very much in evidence.

Paton, C. I. (1939). "A swarm of *Pieris napi* in the Isle of Man." Entomologist, 72: 236.

On the south coast near Balladoole the butterflies were everywhere, seven or eight on small heads of ragwort.

Haines, F. H. (1939). "*Sphinx pinastri* L. (Lep.) in Hampshire." Ent. Mon. Mag. 75: 185.

The penetration of this rare hawk-moth into Hampshire from east Dorset continues.

Hulls, L. G. (1939). "Further observations on *Acherontia atropos*." Entomologist, 72: 249–56.

In 1938 migrant moths visited a strip of the south coast extending at least from Bognor Regis to Portsmouth, and probably farther. It seems evident that they laid their eggs on the first potato plants encountered, for, in practically every instance, the larvae and pupae were found in fields adjacent to the sea. Colour forms of larvae are described and figured, a graph of the loss in weight of the larva between cessation of feeding and pupation, and notes on the pupa and imago are given.

7. Reports of organizations

Lancashire and Cheshire Fauna Committee (1939). Twenty-fifth Annual Report and Report of the Recorders for 1938. 62 pp.

Detailed records (dates, places, some habitat notes and records of changes in numbers) for mammals, reptiles, Amphibia, birds, insects and mites. Some bird ringing records. Special reports on the distribution, habitats and status of reed-warbler, turtle-dove and tufted duck. Reed-warbler found almost always associated with *Phragmites* in Cheshire. Status of various Lepidoptera this year (a bad one for collectors). An important list of mites, many of them parasitic on bird and other hosts (whose names are given), compiled by C. D. Radford. Also a long list of various insects by H. Britten, containing very brief habitat notes.

Dove Marine Laboratory, Cullercoats, Northumberland (1939). Report for the year ending 31 July 1938, Third Series, No. 6, 45 pp. (Marine Laboratory Committee of King's College, Newcastle-on-Tyne, Price 5*s*.)

Herring and salmon investigations are continued and experiments are recorded on the transplanting of mussels for use as bait. A list of anemones and other Anthozoa of the Cullercoats district contains habitat and breeding notes.

Anon. (1939). "Marine biology in the Firth of Clyde. Semi-jubilee of the Scottish Marine Biological Association." Scot. Nat.: 89–93.

The work of the Scottish Marine Biological Association since its foundation in 1914 is briefly reviewed. Before 1923, systematic and physiological studies on Echinoderms, Coelenterates and Crustacea were carried out. But since that year the work has been mainly concerned with plankton studies, especially with the relation of physico-chemical conditions to its occurrence and growth, correlated with which the composition, formation and bacterial population of muds on the sea floor and the biology of young herring have been investigated. Shore ecology, especially that of Mollusca and Crustacea, has been closely studied, chiefly in Kames Bay, Millport, which is a rich feeding ground for young fish that come in, chiefly at night, with the tides. Other work has included studies on the growth of lobsters, the relation and abundance of the fauna to the nature of the sea floor, the life history of Euphausids and the protection of timber from marine boring organisms.

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING IN THE UNIVERSITY DEPARTMENT OF BOTANY, OXFORD

2–4 January 1940

Soirée in the Department of Botany

On the evening of Tuesday, 2 January, about sixty members and guests were entertained at a soirée arranged in the Department by Prof. and Mrs Osborn. A long and interesting series of exhibits was displayed illustrating plant and animal ecology being done in Oxford. An exhibit by Dr J. F. Hope-Simpson illustrated the variation in plants from chalk grassland. Forms of *Leontodon hispidus*, *Plantago lanceolata*, and *Poterium sanguisorba* from different natural habitats were shown to retain their differences in garden culture. Dr and Mrs J. L. Harley gave maps and photographs of the vegetation of a small raised bog at Thornton Mire in the limestone district of Yorkshire. It had a central *Callunetum* surrounded by belts of *Caricetum paniceae* and *Juncetum acutiflori*. Peat profiles recovered by boring showed Phragmites peat and wood peat of fair thickness below the acidic peat. Very extensive mapping and photography was shown by Dr E. W. Jones of the vegetation of Pipley Swamp, Studland Heath. It lies at the head of a valley drowned by marine transgression and shows three zones of *Sphagnetum*, *Molinietum*, and *Phragmitetum*. Very interesting profiles of the valley deposits indicated the results of the marine invasion, and specimens illustrated the root systems of plants from the different zones. Dr Jones also showed the results of a detailed transect through Bagley Wood, Oxford, in which a range of soil types was reflected in a vegetational zonation, and he also demonstrated an apparatus for photoelectric measurement of light intensity in the field, by means of a photoelectric cell suspended downwards above a standard reflecting surface.

Dr A. R. Clapham showed photographs illustrating a transect across the New Forest valley bog at Matley Stream, a site visited by the Society during the Summer Excursion. Prof. Osborn also showed a long series of photographs illustrating the vegetation types seen by the party on its summer visit to Studland Heath. He also showed specimens of *Isoetes echinospora* from Little Sea, *I. Drummondii* from Australia and *I. hystrix* from Corsica. Mr Day had set out a series of scale drawings of the root systems in plan and elevation of different species of poplar growing in soils with impeded drainage. The most extreme soils were a fen peat and a Weald clay, and these showed a very superficial root development above the water-table, in strong contrast to that in freely drained sandy drift over chalk at Thetford. An intermediate type was on boulder-clay in Northants. Dr A. R. Clapham showed an extensive series of herbarium specimens illustrating the species of jointed rushes on which he worked with Mr Timms, and the ecology of which he later described to the meeting. They included *Juncus articulatus* L., *J. acutiflorus* Ehrh., the hybrid between these two, *J. obtusiflorus* Ehrh., and an undescribed form of uncertain status, called "large 80" from its chromosome number.

During the course of the evening Prof. Osborn gave a short talk, illustrated by his own very attractive lantern slides of the visit of the eighth I.P.E. to Morocco. He alluded to the topography, administration, peoples, soils and vegetation, drawing many parallels with arid southern Australia. He emphasized particularly the semi-arid soils with a heavy travertine limestone in the *B* horizon, and the frequent removal by erosion of the *A* horizon.

The Annual Meeting

The twenty-sixth Annual Meeting of the Society was held in the Department of Botany of the University, Oxford, on the following day, Wednesday, 3 January, at 10 a.m., the President, Prof. A. G. Tansley, occupying the chair.

The minutes of the last Annual Meeting were read and confirmed, and apologies for absence were reported.

Mr Summerhayes made a provisional estimate of the financial position of the Society at the end of the year's work, and said he expected a substantial favourable balance. He drew attention to an increase in sales to non-members of the *Journal of Ecology*. A very loudly applauded vote of thanks was then given to the two Hon. Treasurers for their "subterranean" activities for the Society. It was proposed by Dr Varley and carried *nem. con.* that Messrs William Norman and Son be reappointed auditors to the Society for 1940. It was proposed from the chair and carried unanimously that the Council's recommendation be adopted, to make a grant of £10 to the Fresh-water Biological Association, with a warning that circumstances might not allow the Society to repeat the grant. Dr Turrill having explained that it had unfortunately become necessary to give up during 1940 the experiments of the Society successfully carried on by himself and Mr Marsden Jones since 1928, it was agreed to make a further grant of £5 to enable the Transplant Experiments to be closed, and further action was left in the hands of the Council.

The report of the Hon. Secretaries as adopted by the Council was then approved.

Hon. Secretaries' Report for the Year 1939

The twenty-fifth Annual Meeting of the Society was held in the Botanical Department of University College, London, on Saturday, 6 January. On the previous evening a soirée had been given in the department to some eighty members and guests: a series of interesting exhibits had been shown, and Sir Arthur Hill had given a short talk on flower movements.

The Annual Meeting was held on the Saturday, and after the business meeting the President opened an extremely successful discussion on the Reciprocal Relationship of Ecology and Taxonomy, which was continued through the afternoon. The Society is very grateful to Prof. Salisbury and Prof. Hill for their kindness in having given the Society once more the generous hospitality of their department.

Following upon the success which attended the holding of an additional meeting at Easter 1938, a similar additional one-day meeting was held on 4 April in the Metallurgical Lecture Room, Imperial College of Science, South Kensington. Prof. Tansley gave the Presidential address on "British Ecology during the past quarter-century: the Plant Community and the Ecosystem". A series of five papers on diverse ecological topics followed. Our warm thanks are due to Prof. Brown and Mr G. E. Blackman for making possible such an extremely successful meeting.

The Summer Meeting was held in Southampton from Wednesday, 16 August, to Sunday, 20 August. In extremely favourable weather conditions about thirty members and guests made excursions to Studland Heath, to Forestry Commission areas of the New Forest, to shingle spits and salt-marshes at Hurst Castle and Warren Point, and to a group of New Forest valley bogs. On each of three evenings short papers were given on the geology and topography of the district, and the ecology of the areas visited: in addition exhibits had been set out in the Botanical laboratory, and on the last evening Prof. and Mrs Mangham kindly entertained the Society in their home at Nursling. Those who were present look back on the meeting as exceptionally pleasant and instructive, and the Society expresses its sincerest thanks to our Southampton hosts, particularly Prof. Mangham, and to our guides and instructors, notably Mr D. W. Young, who so ably took charge of the New Forest woodland excursion.

In the past year two numbers of vol. **8** of the *Journal of Animal Ecology* have been issued, appearing in May and November, and containing respectively 225 and 188 pages. Twenty-one original papers with 11 plates, in addition to reviews, the Society's notices, and 343 notices of publications on Animal Ecology were issued in them.

Two numbers of the *Journal of Ecology* have been issued since the last Annual Meeting: they appeared in February and August, and contained respectively 261 and 289 pages. Twenty-one original papers were published with 27 plates, as well as notices, reviews, and the obituary of Prof. Carl Schröter.

The Society's transplant experiments at Potterne have continued to give very satisfactory results in the hands of Mr Marsden-Jones and Dr Turrill.

Since the last Annual Meeting the membership of the Society has remained unchanged at 361 members, 16 members having died or resigned, and 16 others having been elected. Of the present membership list 193 members received the *Journal of Ecology* alone, 116 the *Journal of Animal Ecology* alone, 52 both journals, and 1 neither.

The Council has decided that for the present it will continue to organize the meetings and publish the journals of the Society as before the outbreak of war. It hopes that members will also continue, so far as they are able, to support the Society actively despite the difficulties of these times.

The meeting then proceeded to the election of officers as follows:

President: Mr C. Diver (Prof. Tansley retiring).
Vice-Presidents: Dr A. S. Watt (Prof. Hardy retiring) and Dr O. W. Richards.
Hon. Editor of the Journal of Ecology: Prof. W. H. Pearsall.
Hon. Editor of the Journal of Animal Ecology: Mr C. S. Elton.
Hon. Secretaries: Dr H. Godwin and Dr G. C. Varley.
Ordinary Members of Council: Prof. A. G. Tansley, Mr J. S. L. Gilmour, Prof. T. G. Osborn, Mr D. Lack (all for four years), Dr E. S. Russell and Mr F. T. K. Pentelow (re-elected for one year).
Retiring Council Members: Prof. A. C. Hardy and Dr W. B. Turrill.

In the absence of the new President and both Vice-Presidents the retiring President was voted into the chair.

The Hon. Secretaries announced that arrangements were in hand to hold a one-day meeting of the Society in London at Easter, and to hold the Summer meeting in the south-west at either Exeter or Plymouth: further arrangements were left to the Council. The business closed with a very hearty vote of thanks to the two Hon. Editors and the two Hon. Secretaries for their unremitting work on the Society's behalf.

At about 11 a.m. the meeting proceeded to a series of short papers. Prof. A. C. Hardy gave an extremely interesting account of the aerial drift of insects across the North Sea. Nets carried by vessels crossing the North Sea caught many live insects, particularly aphids, and by noting the time and place of capture it was possible to get some idea of the part of the land from which they had come. An average insect population of about 137 millions was reckoned for a central area of the North Sea between sea level and 300 ft. The following took part in the discussion: Prof. A. G. Tansley, Dr G. C. Varley, Dr J. Z. Young, Dr C. B. Williams, Dr H. Godwin, Mr J. S. L. Gilmour, Dr H. C. Gilson, Miss M. F. Mare, and Mr D. Chitty.

Dr A. R. Clapham then gave an account of the ecology of jointed rushes in the Oxford district. *Juncus obtusiflorus* (=*subnodulosus*) grows in the valley fens and hillside fens where there is calcareous water and a water-level maintained high throughout the year: *Juncus acutiflorus* (=*sylvaticus*) is abundant but not dense in meadows beside the Thames, where it is flooded in winter but dry in summer, and where grazing is only light. *Juncus articulatus*

(=*lamprocarpus*) and the hybrid between *J. articulatus* and *J. acutiflorus* are abundant in the grazing meadows, where they seem to resist grazing by virtue of the semi-prostrate lower internodes, the rooting and branching from basal nodes, and the vivipary from inflorescences. In the discussion which followed Prof. A. G. Tansley, Dr P. W. Richards, Mr V. S. Summerhayes and Dr J. H. Harley took part.

There then followed an account by Mr T. G. Tutin of Plant Associations in Submerged Habitats. Mr Tutin described how, as an outcome of his work on the Percy Sladen expedition to Lake Titicaca he had come to doubt the validity of the concept of succession of the lake vegetation to the same climax as the vegetation of the surrounding land. He considered the lake to be a distinct climatic region with its own seres leading to a climax of large brittle-stemmed plants, and proposed the term "limnosere" for this succession, as distinct from the term "hydrosere" which he thought should be restricted to "pond" successions. The "thallassiosere" in the sea was equivalent to the limnosere, and both had under-water climaxes. The extremely wide prospect opened by these suggestions was commented on in the discussion by Dr H. Godwin and Prof. W. H. Pearsall.

Dr J. F. Hope-Simpson then gave an account of the results of recently re-examining the areas of chalk-grassland originally described by Tansley and Adamson in 1919-20. Removal of rabbit-grazing from most communities had led to *Festucetum rubrae*, *Brometa* had changed to the same community, and mixed grassland had become *Brachypodietum*. With increased grazing, communities dominated by *Festuca elatior* or *Arrhenatherum* as well as Calluna chalk-heath had changed to *Festucetum ovinae* or *Agrostido-Festucetum*. These and other changes were demonstrated by records of objective sampling, and by pairs of photographs representing identifiable areas at the beginning and end of the period concerned. Dr A. R. Clapham and Prof. A. G. Tansley spoke in the discussion.

The meeting was continued after lunch with Dr W. B. Turrill in the chair. Dr E. W. Jones gave an account of the factors controlling the distribution of beech and spruce in the Black Forest and Vosges Mts. He pointed out that despite the very great similarity between these two mountain regions in topography and geology the spruce is restricted in the Vosges to very small and localized areas, so that the beech there rises to the tree limit instead of the spruce. Dr Jones inclined to the view that the effect of low winter temperatures was to rob the beech of competitive power against spruce in an easterly and continental direction, thus permitting spruce to extend in a way it cannot in the Atlantic climate of the Vosges.

Prof. A. G. Tansley then took the chair for the opening of a discussion on the Application of Ecology to Present Economic Problems. Mr C. S. Elton described the work which the Bureau of Animal Population was doing to control rats, mice, and rabbits, which use up a large amount of human food "at all stages from the farm to the breakfast table, and possibly beyond". He stressed the importance of a knowledge of the structure of populations in this respect, and the importance of encouraging biological surveys. Mr William Davies stressed the enormous importance of grassland productivity in British agriculture, and described the methods and results of an extensive survey of grasslands of England and Wales, based upon estimates of floristic composition. The vast bulk of this grassland, he said, is of very low productivity, although this could be greatly improved by suitable management.

After an interval for tea provided by our Oxford hosts, the discussion was resumed. Dr Mortimer read and expounded a report from Dr Worthington discussing the productivity of fresh water in both natural and artificial ponds. The use of sewage effluent for manuring the waters was mentioned, and special reference was made to the cultivation of carp and eels. Mr Day said that the war would cause a great deal of clear-felling of woodland, and that ecologists could best operate in advising on the problems of the planting which would have to follow, particularly in relation to the cultivation of exotic trees and the innumerable difficulties raised by the relegation of the forester to the lower grade soils, where factors of

excess or deficiency in the habitat operate with special severity on the woodlands. Dr J. F. Hope-Simpson then made a series of specific suggestions as to treatment likely to improve the southern chalk grassland. He suggested attempts to recover to good grazing land now under *Bromus erectus* or *Brachypodiun pinnatum*, rabbit control in areas of severe overgrazing, and the trial of *Dactylis glomerata*, *Phleum pratense* and *Trifolium repens* in establishment of cover on bare areas. Seasonal grazing in relation to the moss/forb balance was emphasized.

Prof. T. G. Osborn asked how the members of the Society could utilize their special knowledge, and hoped for collaboration with scientists already engaged on specific war tasks. He stressed the value of autecological studies in the short-term investigations called for by present circumstances. Dr H. Godwin deplored the gap between the Scientific Advisory Council and the working scientists and wished to bring pressure on the Government departments to make use of biological scientists. Mr W. Davies pointed out the necessity on our part of saying exactly what we are able to do. Dr C. B. Williams and Dr Mortimer also spoke. After some discussion Dr Godwin proposed the following resolution, which was seconded by Dr Clapham and carried unanimously: "That this Society, either alone or in co-operation with other scientific bodies, should take steps to urge upon the Government a more active utilization of the services of biological research workers in the present emergency." It was further agreed "That the Council be asked to implement this resolution."

Dr O. W. Richards then raised the question of the publication of material for a biological Flora. Reference was made to the scheme already begun by the Society, but the general feeeling was clear that publication of some material should be put in hand at once. Dr Clapham proposed, and Mr Summerhayes seconded, that the council be asked to take action upon this decision, and this was agreed unanimously.

At 10.15 a.m. on the following morning, 4 January, the meeting was resumed with Dr O. W. Richards in the chair. Mr C. B. Goodhart gave an account of the ecology of estuarine amphipods based on work in the neighbourhood of Hurst Castle. He gave a series of distribution maps and verbal descriptions of the habitats of several species of the genera *Melita*, *Corophium* and *Gammarus*. These habitats showed a great range of salinity conditions. There followed an interesting discussion in which Dr O. W. Richards, Dr D. H. Valentine, Dr G. C. Varley, Prof. A. G. Tansley, and Miss F. M. Mare took part.

Prof. A. G. Tansley then took the chair whilst the Vice-president, Dr O. W. Richards, gave a résumé of his quantitative studies on the population of the Cabbage White butterfly at Slough. The problem was defined as that of estimating numbers with a known degree of accuracy, and it was shown how it was possible to interpret the census data so as to arrive at estimates of the proportion of insects destroyed by various agencies such as predators, birds, disease and climate. Prof. A. G. Tansley, Dr G. C. Varley, Dr G. D. Hale Carpenter, Dr E. W. Jones, Dr H. C. Gilson, Mr G. E. Blackman, and Dr J. F. Hope-Simpson took part in the discussion afterwards.

Dr Richards then resumed the chair, and called on Dr D. H. Valentine for his paper on the distribution of the Primrose and Oxlip in the woods of eastern England. Dr Valentine described the examination of a wood with a central pure oxlip population surrounded by primroses, with an intermediate belt of hybrids. Hybrids were rare in the primrose areas, but abundant in the oxlip area. The explanation was shown to depend on the fact established esperimentally by the speaker, that the cross with the primrose as female parent yields no viable seed, whereas the cross with oxlip as the female parent produces a fair proportion of hybrid offspring. Thus the primrose is invading the oxlip population by its pollen, and will tend to replace oxlip. In the interesting discussion raised by this account the following members spoke: Dr C. B. Williams, Dr G. C. Varley, Mr G. E. Blackman, Dr W. B. Turrill, Prof. A. G. Tansley, Dr O. W. Richards, Dr A. R. Clapham and Dr J. S. L. Gilmour.

Mr H. G. Veevers then gave an account of the different methods which have been used to count gannet populations in the twenty-two colonies known in the world. The work done in conjunction with Mr James Fisher in the 1939 census showed the total population of the species to be about 170,000. Accounts of the history of individual colonies were employed to illustrate the nature of the factors now operating to determine the size and position of gannet populations. Dr O. W. Richards, Dr C. B. Williams and Mr J. S. L. Gilmour asked questions at the end of the paper.

Dr J. L. Harley then described the results of his studies on woodland soils under beech forest in the Chilterns. He compared the three major soil types: Escarpment, *A* type Plateau, and *C* type Plateau in respect of total nitrogen and carbon, carbon dioxide emission, soluble carbon, fungal and bacterial content, rate of mobilization of nitrogen, and available calcium. In all these respects there is the same relation of the three soil types, highest values being in the escarpment soils, and falling off to the Plateau *C* soils. The low density of roots in the surface soil of Plateau *A* type was due to the absence of the restricting factors present in the other soils, shallowness in the one and biological poverty in the other. Heavy mycorrhizal infection was shown to be restricted to the two Plateau soils. Dr Mortimer, Mr Day, and Mr G. E. Blackman raised questions afterwards.

Dr V. J. Chapman then gave an account of the relation of plants to the West Indian shoreline. By lantern slides and specimens he illustrated the beaches and dunes made of "Halimeda sand" with their vegetation. The mangrove vegetation of the shore he related to three soil types, reef, mud, and a fibrous "marine peat" formed slowly in the absence of silting. The low tidal range prevents any pronounced zonation with rising shore-level. Dr E. W. Jones and Prof. T. G. Osborn spoke in the discussion afterwards.

At the close of the meeting Dr O. W. Richards thanked Prof. and Mrs Osborn very heartily for all the trouble they had given themselves to make the meeting so enjoyable, and Dr Godwin expressed a similar gratitude of the Society to Dr Clapham who had borne the burden of the local arrangements, and to the cheerful and efficient laboratory staff.

SUMMER MEETING AT SOUTHAMPTON

16–20 August 1939

Following the kind invitation of Prof. Mangham the Summer Meeting of the Society was held in Southampton, and the opening was held in the Department of Botany at 8.45 p.m. on the evening of 16 August. Prof. W. Rae Sherrifs very kindly gave the Society an illustrated account of the geology and topography of the country round Southampton, and at the end of the evening Mr Diver outlined the programme for the excursion on the morrow.

Thursday, 17 *August*. Under the competent leadership of Mr C. Diver and Dr E. W. Jones the party visited Studland Heath. They were there shown the extensive dune system of known age overlying Bagshot Sand. These dunes differ from most coastal dunes in the extremely low initial content of lime, which seems to be responsible for the absence of all intermediate seral stages between *Ammophiletum* and Calluna heath, as well as the very scanty population of fresh-water snails, and the virtual absence of larks and meadow-pipits. Larks are present on the Bagshot beds nearby. The party was shown many interesting developmental stages both of the dunes themselves and of the wet hollows between them. Captain Diver told us about the distribution of grasshoppers in the area, and these insects and their allies got more attention from the zoologists than any other group of animals, because the group is so well represented in these parts by species which are normally regarded as rare. Various members collaborated in the study of grasshoppers, and became expert in their detection by sound alone. It may be worth mentioning that a number of specimens of the rare wasp *Odynerus basilis* Sm. were seen, apparently burrowing in the sand. The party had lunch by the shores of Little Sea, and the magnificent weather encouraged almost all the

party to enter the lake, ostensibly to make leisurely investigation of the bottom flora with its carpet of *Isoetes echinospora*. The party then went on to examine the vegetation of Pipley Swamp at the southern end of Little Sea. We were then shown Brand's Bog, a very interesting example of a valley bog, showing a well-marked pool and hummock structure, and a rich Sphagnum flora including *S. auriculatum* var. *sanguinale*, *S. papillosum*, *S. tenellum*, *S. compactum*, *S. pulchrum* and *S. cuspidatum*. *Erica ciliaris* was present on the hummocks. The lower slopes of this bog showed an unusual transition to salt marsh vegetation, through a bog vegetation mixed with *Schoenus nigricans*, then a belt dominated by *Schoenus*, and finally *Juncetum maritimae*.

After tea at the ferry the party drove back to Southampton, and in the evening attended a meeting in the Department of Botany. Mr T. N. Retford gave an account of the Hydrography of Poole Harbour, carried out by the University Department of Geography. The 15 square miles of the harbour is a drowned valley, and has a tidal range of only 2 to 6 ft. Mr Retford discussed the problems of silt movement in the harbour, and suggested that it had no direct marine origin. The role of *Spartina Townsendii* in mud fixation was stressed, the rhizomes of this plant growing at 6 to 18 in. above mean sea-level. It appeared that where channels were now being filled the material was coming from the erosion of unprotected mud flats at low water. Considerable general discussion followed the paper, and then Miss K. Boswell gave an account of the topographical changes in the developing shingle spit system at Warren Point. A series of maps of different dates established that practically all its growth had been made since 1907.

Friday, 18 *August*. The party assembled at Denny Wood on the Beaulieu Road, and Mr D. W. Young explained some of the major ecological features of the New Forest woodlands. There probably had always been heath on the Plateau Gravels and forest on the clays and better soils, with a spiny shrub zone between the two. The absence of coppice shrubs was due to grazing beneath the trees. Pines, introduced in 1783, were now invading the heaths rapidly, and reduction in the herds of deer since 1850 had caused much extension of the holly, especially in the marginal land. The part first examined of the Denny Enclosure was on Barton Sands, and the soil profile was exposed in deep pits which showed only a very slight tendency of the soil to podsolization. These inspection pits in the Forest proved to be very efficient traps for ground beetles, and there was some competition to be first down the hole to discover what had been caught. The party walked to an area above the Headon Beds, where the soil is less satisfactory, bearing *Leucobryum* and *Polytrichum formosum*, with no *Euphorbia amygdaloides* and no regeneration of ash. The soil profile here had a narrow *B* layer with humus and iron pan over gravel. At Vinney Ridge the party saw planted exotic species of many kinds with good natural regeneration. At Knightwood there was 15 in. of peat over Barton Sands with some clay: the accumulation in the *B* layer was irregular and there was strong gleying. This had been planted with Scots pine which was not, however, regenerating. The Bolderswood enclosure on Plateau gravel over Barton Clay carried *Pseudostuga Douglasii*, *Sequoia sempervirens* and Sitka spruce up to 120 ft. high after only seventy years' growth, with a great many fine specimens of other exotic conifers. The party returned to Southampton after tea at Lyndhurst.

In the evening, in the Department of Botany, Prof. Mangham gave an outline of what the excursion might expect to see on the following day. He paid special attention to the progress of *Spartina Townsendii* on this coast, and the growth of the shingle spits. Dr H. Godwin followed with an account of the submerged peat beds revealed in the excavations for the King George V Graving Dock at Southampton. Pollen analyses showed that the beds had begun in the Pre-Boreal period and had continued until marine transgression had intervened not earlier than middle or late Atlantic times. Possible links with the work on Poole Harbour and with Dr Jones's borings in Pipley Swamp were suggested.

Saturday, 19 *August*. The party visited Warren Point, at the end of the Beaulieu River, where Miss Boswell demonstrated the movements of the shingle spits and mud banks. The older ridges supported *Cirsium tenuiflorus*. In a depression behind the shingle ridges was shallow water, said to be fresh enough for cattle to drink. Here was a dense stand of mixed *Scirpus maritimus* and *S. tabernaemontani*. Cutting for hay-rick thatching was in progress, and this was said to favour the former species against the latter. We went on from here to Hurst Castle shingle spit. Here the method of detecting grasshoppers by sound, learned on the South Haven excursion, revealed in the marshes a colony of the grasshopper *Metrioptera roeselii*. Apparently the species had not previously been found on the South coast, the nearest station being the north Kent coast.

In the evening Prof. and Mrs Mangham entertained members to coffee at their riverside home at Nursling.

Sunday, 20 *August*. Under the direction of Dr A. R. Clapham and Dr H. Godwin the party was taken over three representative valley bogs of the New Forest. The first was at Matley Bog, where the flood plain of the central stream has a shallow, silty, basic peat, and bears tall alder wood "carr", very like that in the East Anglian fens. By a series of transitional zones on either flank this passes into the tussocky *Sphagnetum* maintained by drainage flushes from the hillside. In the "splash zone" outside the fen wood there was abundant *Ludwiga palustris*. The region next seen was part of the broad outflow channel of Denny Bog, on the south side of Beaulieu Road Station. The extensive floating vegetation mat over shallow water, and the thin central line of fen wood were very striking. The last of these sites was at Crane's Moor, north of Burley. Here the influence of the hillside drainage was very great, and a series of terraces showed most interesting pool and hummock structure. In the bottom of the valley, relict Phragmites piercing the *Sphagneta* indicated the former deep channel of the stream, and eutrophic influences were more widely indicated by the prevalence of *Schoenus nigricans*.

These New Forest bogs include the rare localities for the large grasshopper *Mecostethus grossus*, several specimens of which were captured.

A communal farewell took place on the Ringwood Road about 3 p.m., and the President expressed the gratitude of all the party to Prof. Mangham and to the organizers and guides who had made this Summer Excursion one of the most pleasurable in the history of the Society.

A full address list of the Society's members is printed in the *Journal of Ecology*, Volume 28, No. 1, February 1940.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1939

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance:		
Members taking *Journal of Ecology* only	228 17 3	
Members taking *Journal of Animal Ecology* only ...	135 19 6	
Members taking both Journals	118 11 0	
Associates	15 0	
		484 2 9
Interest on Investments	46 15 0	
Interest on Deposit Account	10 6	
		47 5 6
Index volume to *Journal of Ecology*, vols. I–XX:		
Sales	8 4 0	
Expenses	1 5 6	
		6 18 6
		£538 6 9
Journal of Ecology, 1939:		
Sales: Current vol. **27**, 1939	583 10 6	
Back volumes and parts	37 10 5	
Reprints of papers	53 17 6	
		674 18 5
Advertisement		10 0
Grant: From Crown Agents for the Colonies ...		30 0 0
		705 8 5
Balance (see above, under Expenditure)		147 19 3
		£853 7 8
Journal of Animal Ecology, 1939:		
Sales: Current vol. **8**, 1939	271 18 4	
Back volumes and parts	37 0 9	
Reprints of papers	117 15 6	
		426 14 7
Balance (see above, under Expenditure)		201 3 9
		£627 18 4

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing, Stationery, etc.	13 7 0	
Postages and Travelling	10 18 8	
Bank Charges	13 4	
Soirée Expenses	1 16 7	
Audit	4 4 0	
Clerical assistance	15 0 0	
		45 19 7
Nomenclature of Tropical Forest Communities, Typing Report		4 17 2
Grants:		
Fresh-water Biological Association	20 0 0	
Transplants Experiments Fund	5 0 0	
		25 0 0
Journal of Ecology. Cost *less* Sales		147 19 3
Journal of Animal Ecology. Cost *less* Sales		201 3 9
		424 19 9
Balance: Surplus for the Year, carried forward ...		113 7 0
		£538 6 9
Journal of Ecology, 1939:		
Cost: Paper, Blocks, Printing and Binding		721 19 4
Publishers' Commission		86 3 1
Carriage and Postages		37 1 2
Insurance and Sundry Expenses		8 4 1
		£853 7 8
Journal of Animal Ecology, 1939:		
Cost: Paper, Blocks, Printing and Binding		550 9 6
Publishers' Commission		47 19 11
Carriage and Postages		21 9 3
Insurance and Advertising		7 19 8
		£627 18 4

BALANCE SHEET AT 31 DECEMBER 1939

Assets

	£ s. d.	£ s. d.
Cash at Bank		208 2 2
Journal of Animal Ecology:		
Balance of Publishing Account for 1939, due from Cambridge University Press...		138 0 1
Investments at Cost:		
Brought forward, 31 December 1938	1,072 0 10	
Purchased in March, 1939: £200 of 3½% War Loan	196 16 0	
		1,268 16 10
		£1,614 19 1

Notes *re* Investments:

Totals held, 31 December 1939:	£ s. d.
£1,050 of 3½% War Loan at cost ...	1,070 6 10
£200 of 5% Conversion Loan ...	198 10 0
	£1,268 16 10

The market value of the above Investments at 31 December 1939:

	£ s. d.
3½% War Loan at 93⅛	981 15 0
5% Conversion Loan 108¼	217 10 0
	£1,199 5 0

A further Asset, not valued above, is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) V. S. SUMMERHAYES,
ALEX. S. WATT,
Hon. Treasurers.

Liabilities

	£ s. d.	£ s. d.
Members' subscriptions, prepaid for 1940/41, ...		8 10 0
Library Fund		1 5 0
Journal of Animal Ecology, vol. **8**, No. 2 Balance of Printing Account due		211 18 4
General Revenue Account, Surplus in hand:		
Balance at 31 December 1938	1,279 18 9	
Surplus for Year 1939	113 7 0	
		1,393 5 9
		£1,614 19 1

Audited and found correct and as shown by the Account Books of the Society. The Bank Balance has been verified by Bank Certificate, and also the Investments.

(Signed) WM NORMAN & SONS,
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.

25 *January* 1940